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ARBOREAL OR TERRESTRIAL ANCESTRY OF PLACENTAL MAMMALS

BY R. WHEELER HAINES

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TH. HUXLEY (1880), who first suggested an arboreal ancestry for marsupial mammals, pointed out that several peculiarities of marsupial anatomy could be explained by the supposition that all living forms had been derived from a common ancestor of arboreal habit, similar in structure and mode of life to the modern opossum *Didelphys*. Dollo (1889) used the persistence of traces of former arboreal specialization in the marsupial foot, even in strictly terrestrial forms, to illustrate his law of irreversibility of evolution. Bensley (1901a, b) also supported Huxley's hypothesis. At that time no one considered mammals in general as other than terrestrial in origin. Dollo, in fact, was emphatic on this point: "En effet, personne ne soutiendra que tous ceux-ci ont passé par une phase arboricole. Et quant à ceux qui en sont là aujourd'hui, ce sont des types sporadiques, qu'ont pris naissance indépendement: la chose est évidente."

Matthew (1904) extended Huxley's views to include placentals as well as marsupials. He based his opinion on the slender and flexible build of the Eocene mammals, the long, powerful, "probably prehensile" tail, the freedom of pronation and supination of the forearm, and above all on the supposed opposability of the pollex and hallux. He suggested that the squirrels, monkeys, and tupaiids were primitively arboreal creatures. Matthew added new evidence from time to time, particularly in his study of the creodonts of the Bridger Basin (1909); and eventually (1937) he restated his hypothesis in great detail, with much new material from Paleocene strata, and again emphasized the presence of "opposable" or "semi-opposable" pollices. His suggestions have been very generally accepted. Thus Gregory (1913) derived the Eocene lemuroids from "opossum-like arboreal placentals" that also gave rise to other orders, and Simpson (1937) stated that Matthew's theory had "not been significantly shaken." Romer (1945) suggests that the early placentals "were inconspicuous forest dwellers and nocturnal to some degree at least. Certain characters in their descendants (such as the frequently divergent pollex and hallux) suggest an early arboreal habitat, although in most placental types terrestrial life seems to have been taken up at an early date." Le Gros Clark (1949) speaks of an "arboreal mammalian prototype." None of these authors, however, has discussed Matthew's anatomical evidence in any detail.

On the continent the conception of an arboreal ancestry for placentals was reached independently from a study of the foot rather than the hand. Klaatsch (1913) and Weidenreich (1921) compared the union of the second and third toes that occurs normally in the gibbon *Symphalangus* and occasionally in man with the syndactyly found in marsupials such as *Phalanger*, and suggested a common origin for this specialization, which was associated

with a prehensile hallux and implied an arboreal habitat. Böker (1927) developed this suggestion as part of his general "Schweilentheorie" of the limbs, and figured as "das Ursäugetier" a lizard-like creature, forced to live in the "Gewirr von Stengeln und Ästchen" of the bushes that had by Permian times replaced the earlier swamps, creeping along a thin branch, gripping it with the pollex and hallux opposed to the other digits. The body was raised as it was forced forward, but "dann musste der Körper aber wieder auf die Unterlage aufgelegt werde, bis die Hände und Füsse neue Angreifpunkte gefunden hatten." Lorenz (1927) explained the greater breadth of the hand in the fetus of *Tupaia* as compared with the adult by a loss of opposition in the hallux as the claws came to be used for climbing, and Panzer (1932) showed in great detail how all climbing animals might be derived from Böker's "primäre Klammerklettern." Panzer referred to a citation of Matthew's work in a general textbook, otherwise there is no mention of the fossil material in this continental literature.

Gidley (1919), however, believed that the simple divergence of the first metacarpal or metatarsal from the others, as found in *Pantolambda*, *Euprotogonia*, *Claenodon*, and *Dissacus*—that is, in all the early forms the structure of whose hand was known—was not in itself evidence of opposability of the pollex or hallux. The "power to grasp or hold, by opposing the first digit to the others," was not found in placentals before the Middle Eocene, and then only in species of a single order, the Primates. There has been no serious discussion of the point since Matthew's (1937) final restatement of his views. Hooton's (1946) conception of a "primitive ground dwelling mammal, provided with a long, pointed snout," a conception based on the work of Wood Jones (1929), was unique in modern literature; but recently Gregory (1951) has suggested that "the remote and still largely unknown Cretaceous ancestors of the placental mammals were not as much specialized for arboreal life as were the ancestral marsupials; but they were able to scratch, dig, grasp, or climb."

Simpson (1945) spoke of the arboreal tupaiids as "the most nearly generalized of surviving Theria," while Gregory (1951) proposed the terrestrial insectivore *Hylomys* as the most primitive living placental. But, as regards the structure of the hand, it has been found that the Insectivora, including the tupaiids, show specializations that preclude their being regarded as representing the primitive placental stock (Haines, 1955).

In the present paper the hand of *Herpestes ichneumon*, the common Egyptian mongoose, is described as a typical terrestrial form, only slightly modified for cursorial locomotion. Comparisons with other animals follow, and the various types of grasping hand are reclassified. Gidley (1919) himself stated that "opposability is always accompanied by a special and distinctive arrangement and development of the digital muscles," but at the time he wrote myological information was too limited to enable him to follow out his suggestions in detail. Here data from the classic work of Klaatsch (1888), Whipple (1904), and Kidd (1907) and the several contributions of Wood Jones and Pocock on external form, and from the myological studies of Cunningham (1882), Forster (1916) Straus (1941, 1942a), Haines (1939, 1950) and others have been brought together in an attempt to define the structure of the early placental hand and determine the environment in which its possessors lived.

THE HAND OF HERPESTES

Surface Form

Herpestes is a low-built terrestrial hunter capable of creeping, walking, trotting, and galloping (the leaping gallop of Slijper, 1946). It can burrow, using its blunt claws for dislodging stones and shooting loosened earth back between its legs with both hands used together. It swims instinctively, with its long tail trailing flaccidly behind and its limbs paddling in a fore and aft movement. It can scramble over rock surfaces or run up a rough fence, but cannot climb the smooth trunk of a tree, and is never actually found up trees. It uses its hands for pouncing on insects or crabs, and for holding food as it tears with its mouth, but the hands are not used for fighting or carrying food to the mouth. The tongue and teeth are used for cleaning the fur, and both hands and feet are used for scratching.

The hand (Fig. 1) is stoutly built with short digits carrying smooth terminal pads (*tm.p.*) and is webbed as far as the pads, giving a large surface for digging or swimming. The hand is artiodactyl in type, with digits III and IV subequal, as also are II and V; while I is short, set far back, and provided with a relatively sharp claw, probably acting

as a toilet digit. The palm is bare, and carries a large interdigital eminence (*i.d.e.*) and two proximal pads (*th.p.* and *hy.p.*). All the pads are covered with thick skin, and the animal leaps from heights without hesitation, braking by skidding on the pad surfaces. In walking the pads take most of the pressure and leave prints, though the tips of the claws also touch the ground and can be heard tapping lightly as the animal crosses hard tiles. Carpal vibrissae were not seen in my material, but are figured by Allen (1924) in a specimen from the Congo.

When the hand is open the claws of I and V are turned toward the palm, and when the digits are flexed all the pads come nearer together and the claws of II–V almost touch. Digit I is still set off from the others, but it is not placed opposite to the others, and the animal cannot use it as a thumb for grasping.

Extensor Muscles

The brachioradialis (*br.rd.*) has two insertions on the distal end of the radius, and in addition gives a contribution to the extensor retinaculum (*e.rt.*). The extensor carpi radialis (*e.cp.r*) divides to insert on metacarpals II and III. The extensor digitorum communis (*e.dg.c.*) has four tendons to II–V, agreeing with the description given by Windle and Parsons (1897); there are not five, as Ribbing (1907) stated. Digits IV and V receive additional tendons from the ulnar extensor (*e.dg.u.*). The extensor carpi ulnaris (*e.cp.u.*) arises from both humerus and ulna and passes to metacarpal V, contributing to the extensor retinaculum. The anconeus (*anc.*) passes to the olecranon, and the supinator (*sup.*) to the proximal part of the shaft of the radius. The abductor pollicis longus (*ab.p.l.*) passes from the ulna to metacarpal I, with a slip to the flexor retinaculum (see Fig. 3), and the extensor digitorum profundus (*e.dg.p.*) reaches I–III. A radial sesamoid (*rd.sd.*) is present in the tendon of the abductor pollicis longus, and a set of digital sesamoids (*dg.sd.*) overlies the metacarpo-phalangeal joints.

The anconeus is supplied by its own nerve, which branches directly from the trunk of the radial (*n.anc.*); the remaining extensors by the dorsal interosseous, a branch of the radial (*n.i.o.d.*). The cutaneous supply is from the nervus dorsalis manus radialis (*n.d.m.r.*) and the dorsal cutaneous branch of the ulnar nerve (*r.d.n.u.*).

Flexor Muscles

The pronator teres (*pr.t.*) inserts just below the center of the radius. The flexor carpi radialis (*f.cp.r.*) joins the ligaments on the palmar surface of the carpus and so reaches metacarpals II and III, there being no insertion on I as stated by Ribbing (1938). The palmaris longus (*pl.l.*) spreads out into the palmar aponeurosis (*p.ap.*) and the two heads of the flexor carpi ulnaris (*f.cp.u.*) remain distinct almost to their insertion on the pisiform. The flexor digitorum profundus has a full set of heads, three from the humerus, the condyloradialis (*cn.r.*), condyloulnaris (*cn.u.*) and centralis (*cen.*), an ulnar head (*u.hd.*) from the ulna, and a radial head (*rd.h.*) from both the radius and ulna. The condyloradialis and condyloulnaris soon join, and so do the radial and ulnar heads, so that near the wrist there are the three independent tendons, and these join together before giving the five tendons to the terminal phalanges.

The flexor digitorum sublimis (*f.dg.s.*) takes origin from the combined tendon of the condyloradialis and ulnaris as a simple fleshy belly, and inserts on digits II, III, and IV by tendons that first form rings (*rg.f.s.*) round the profundus tendons, and then split to let the profundus tendons pass through. The tendon to IV is joined by a slip from the flexor digitorum brevis manus (*f.b.m.*), which also provides the whole of the perforated tendon to V.

The epitrochleo-anconeus (*ep.a.*) passes from the medial epicondyle of the humerus to the olecranon of the ulna, and the pronator quadratus (*pr.q.*) is a large muscle occupying two thirds of the length of the forearm. The four lumbricals (*lum.*) insert on the radial sides of the basal phalanges. A strong abductor digiti V (*ab.V.*) passes from the pisiform, and a pair of small muscles arises from the ligaments on the anterior surface of the carpus, an abductor pollicis brevis (*ab.p.b.*) passing to the basal phalanx of I and an opponens (*op.I.*) to the metacarpal and basal phalanx. A palmaris brevis (*pl.b.*) passes across the palm to the region of the hypothenar pad.

The four contrahentes (*cn.*) are crowded onto the capitate at their origins, but spread out to be inserted onto the ulnar sides of the basal phalanges of digits I and II and the radial sides of the basal phalanx and metacarpal of V. The flexores breves profundi take origin from the bases of the meta-

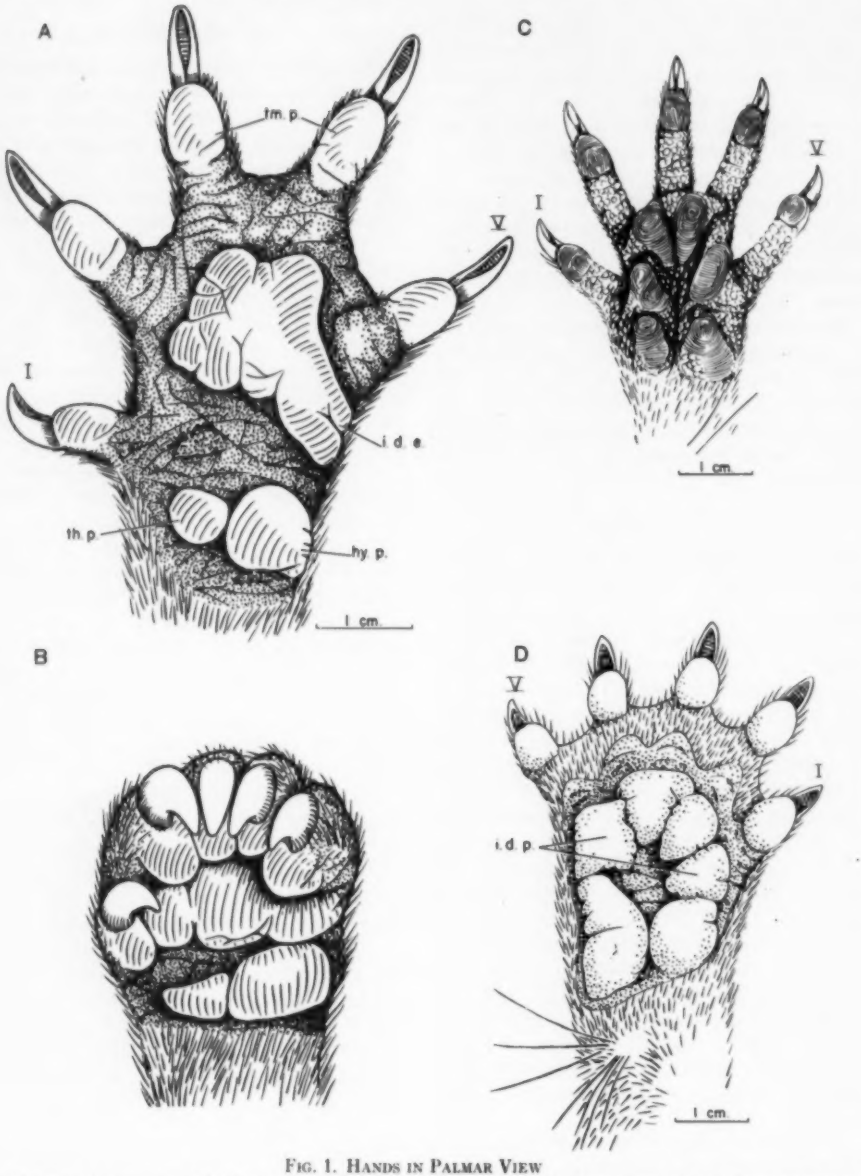

FIG. 1. HANDS IN PALMAR VIEW

A, *Herpestes ichneumon*, with digits spread. B, *Herpestes ichneumon*, with digits flexed. C, *Didelphys virginiana*. D, *Nandinia binotata*.

KEY TO LETTERING

ab.V., abductor digiti quinti
ab.p. b., abductor pollicis brevis
ab.p. l., abductor pollicis longus
anc., anconeus
ax.a., axial artery
br.rd., bracheoradialis
Cap., Capitate
Cen., Centrale
cen., centralis
cn.I,II&V., contrahens I, II & V.

carpals and insert into the extensor tendons of digits II–IV.

The median nerve (*n.md.*), after traversing the entepicondylar foramen with the axial artery (*ax.a.*), supplies the pronator teres, flexor carpi radialis, palmaris longus, and the three heads of the flexor digitorum profundus, and gives a volar interosseous nerve (*n.i.o.v.*) that supplies the radial head of the profundus and the pronator quadratus. In the lower part of the forearm it supplies the flexor digitorum sublimis. It then enters the palm under the flexor retinaculum (*f.rt.*) and supplies the opponens pollicis, the abductor pollicis brevis, and the first lumbrical.

The ulnar nerve passes deep to the epitrochleo-anconeus, then between the two heads of the flexor carpi ulnaris onto the surface of the ulnar head of the flexor digitorum profundus, and supplies all these muscles. After giving the dorsal cutaneous branch to the back of the hand, it enters the palm between the layers of the flexor retinaculum, and splits into a superficial (*n.ul.s.*) and a deep (*n.ul.d.*) branch, divided by a ligament that joins the pisiform and the base of metacarpal IV. The superficial branch supplies the palmaris brevis, the deep the flexor digitorum brevis manus, the three ulnar lumbricals, and all the contrahentes and flexores digitorum breves profundi.

Pronation and Supination

The head of the radius is oval rather than round (Fig. 4, B and C), a shape which might suggest that it is not fitted for turning on the ulna. It is, however, surrounded by a complete annular ligament, and a trial shows that the radius rotates through about 50° on the ulna, and the ulna rocks a further 30° on the humerus. The annular ligament moulds itself to the radius as the bone turns, being itself attached to both humerus and radius by the radial collateral ligament (*l.cl.r.*). In pronation, the position ordinarily adopted in walking or digging, the head of the radius rests snugly in its notch on the ulna (Fig. 4, B), so that the bones are in a "close-packed" position giving maximum mechanical security (MacConaill, 1932), while in supination the head rests on the edges of the notch, and a different area of the head comes into contact with the humerus (*s.cap.*).

The ulnar collateral ligament (*l.cl.u.*) is partly split to reach both radius and ulna. The interosseous ligament (*l.i.o.*) is restricted in extent, but a strong inferior radio-ulnar ligament (*l.r.u.i.*) at-

cn.mt.V., contrahens metacarpi V.
cn.r., condylo-radialis
cn.u., condylo-ulnaris
dg.sd., digital sesamoid.
e.cp.r., extensor carpi radialis
e.cp.u., extensor carpi ulnaris
e.dg.c., extensor digitorum communis
e.dg.p., extensor digitorum profundus.
e.dg.u., extensor digitorum ulnaris
en.f., entepicondylar foramen
ep.a., epitrochleo-anconeus
e.rt., extensor retinaculum
f.b.mn., flexor brevis digitorum manus
f.cp.r., flexor carpi radialis
f.cp.u., flexor carpi ulnaris
f.dg.b.p., flexor digitorum brevis profundus
f.dg.s., flexor digitorum sublimis
f.rt., flexor retinaculum
Hm., Hamate
hy.p., hypothenar pad.
i.d.e., interdigital eminence
i.d.p., interdigital pad
jt.c., joint cavity
l.ann., annular ligament
l.cl.r., radial collateral ligament
l.cl.u., ulnar collateral ligament
l.eto.o., epitrochleo-olecronal ligament
l.i.o., interosseus ligament
ll.wr., ligaments of wrist
l.r.u.i., inferior radio-ulnar ligament
lum., lumbrical
Mg., Magnum
n.anc., nerve to anconeus
n.d.m.r., nervus dorsalis manus radialis
n.f.b.mn., nerve to flexor brevis digitorum manus
n.i.o.d., dorsal interosseus nerve
n.i.o.v., volar interosseus nerve
n.lum., nerve to lumbrical
n.md., median nerve
n.rd., radial nerve
n.ul., ulnar nerve
n.ul.d., deep branch of ulnar nerve
n.ul.s., superficial branch of ulnar nerve
op.I&V., opponens I & V.
p.ap., palmar aponeurosis
pl.b., palmaris brevis
pl.l., palmaris longus
pr.q., pronator quadratus
pr.t., pronator teres
r.d.n.u., dorsal cutaneous branch of ulnar nerve
r.hd., radial head of flexor profundus
rd.sd., radial sesamoid
rg.f.s., ring of flexor sublimis
Sc., Scaphoid
s.cap., surface for capitate
Sc.lu., Scapho-lunar
s.pis., surface for pisiform
s.tri., surface for triquetrum
sty.R., styloid process of Radius
sup., supinator
Td., Trapezoid
th.p., thenar pad
Tm., Trapezium
tm.p., terminal pad
u.hd., ulnar head

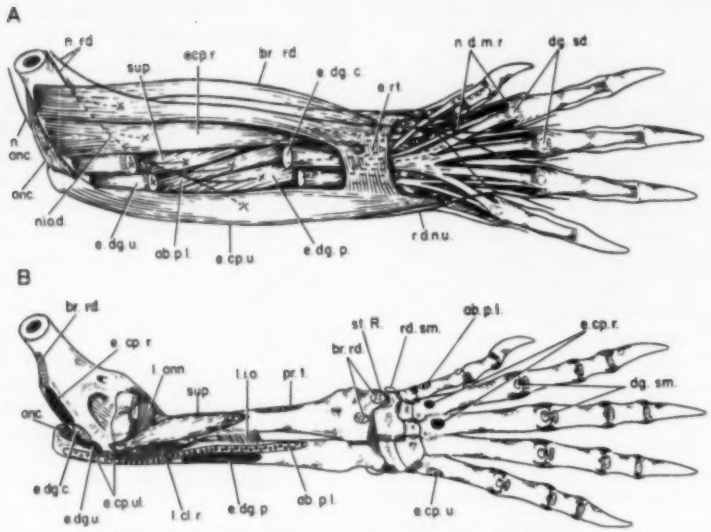

FIG. 2. EXTENSOR MUSCULATURE OF *HERPESTES ICHNEUMON*
A, the muscles; B, the attachments.

taches the bones at the wrist, and a small joint cavity is found between them (Fig. 3, D, *j.c.*).

The Joints of the Hand

The radius and ulna articulate with the scapholunar and triquetral, with the pisiform wedged between the styloid of the ulna and the triquetral. The styloid of the radius is received into a groove on the scapholunar (Fig. 2, B, *sty.R.*) so that considerable flexion and extension are allowed, but little lateral movement. The distal row of carpal bones (Fig. 5), the trapezium, trapezoid, capitate, and hamate, is tied by ligaments to the proximal row so as to allow but limited movement at the mid-carpal joint, and the metacarpals are attached to each other by strong ligaments at their bases. Metacarpal II articulates with three carpals, while I has a restricted saddle-shaped facet, convex antero-posteriorly and concave mediolaterally, that articulates with a corresponding facet on the trapezium. The carpo-metacarpal joints allow flexion and extension and also considerable radial and ulnar deviation, particularly in the case of the first, but there is no special mechanism for rotation.

Walking

In walking (Fig. 6) the hand is advanced near the head, with the scapula displaced and rotated anteriorly and the elbow extended (*a*). The hand is placed flat on the ground with all the carpal pads in contact. As the limb is drawn backward, the elbow is flexed and the digits become extended at the metacarpo-phalangeal joints (*b* and *c*), so that the weight is taken by the interdigital pad. At the end of the pace the scapula is turned back, the elbow is again extended, and the hand "peels off" the ground (*d*) as does the hand of crocodiles and lizards (Schaeffer, 1941; Haines, 1952). The arm swings forward with the elbow flexed to raise the relaxed hand from the ground (*e* and *f*), and the hand is well advanced (*g*), so that it is already moving backward when it meets the ground again. This cycle requires, on flat ground, only simple hinge movements in a fore-and-aft direction, the forearm being in pronation throughout. But when the animal is scrambling over rocks, investigating a hole, or pulling at a stone the hand is seen to turn as the forearm movements are used.

COMPARISON BETWEEN HERPESTES AND OTHER ANIMALS

Surface Form

In *Didelphys*, the genus chosen by Klaatsch (1888), Whipple (1904), and Kidd (1907) to illustrate the primitive mammalian type of hand, the

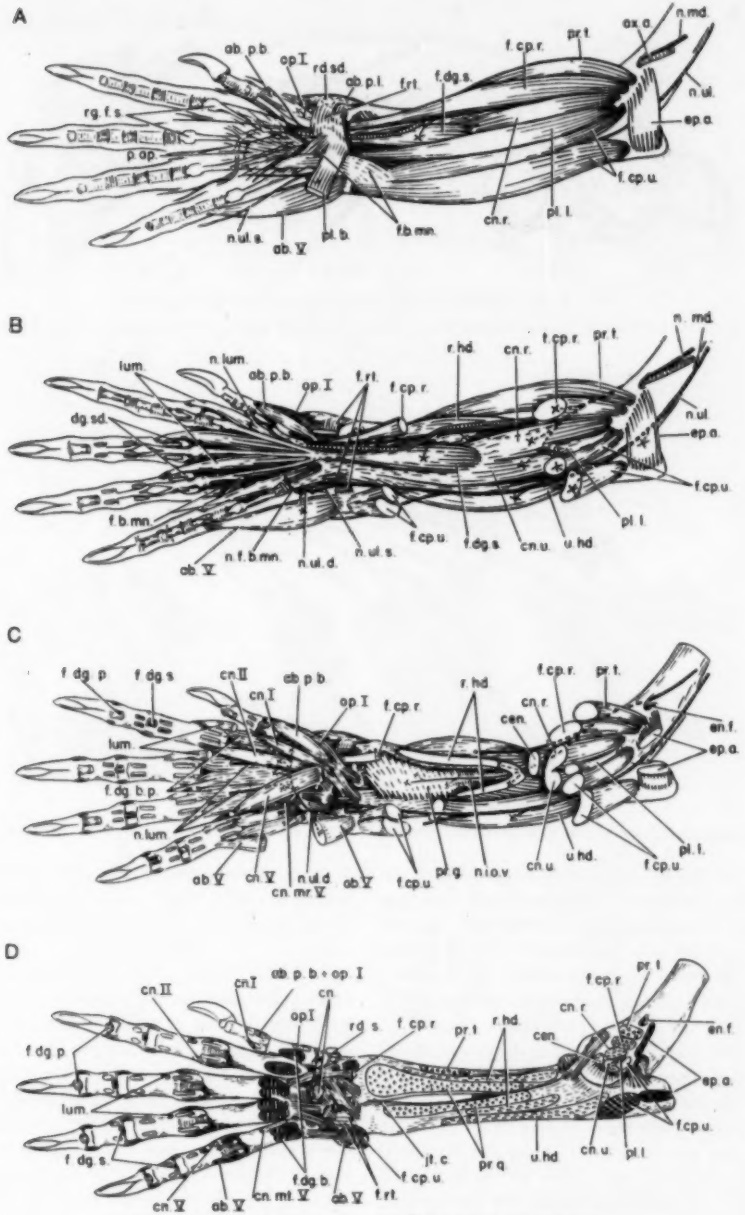

FIG. 3. FLEXOR MUSCULATURE OF *HERPESTES ICHNEUMON*
A, superficial muscles; B, flexors of the digits; C, deep muscles; D, attachments.

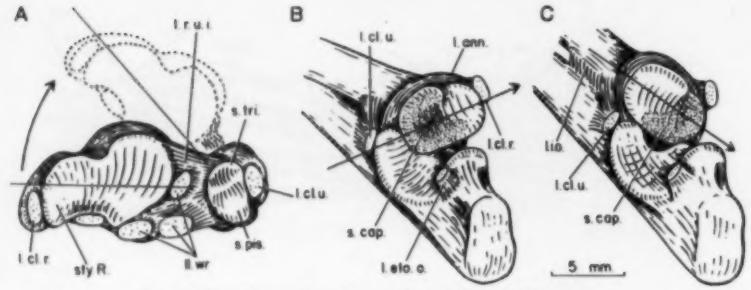

FIG. 4. *HERPESTES ICHNEUMON*, RADIO-ULNAR MOVEMENTS
A, distal radio-ulnar joint, showing range of movement; B and C, proximal radio-ulnar joint.

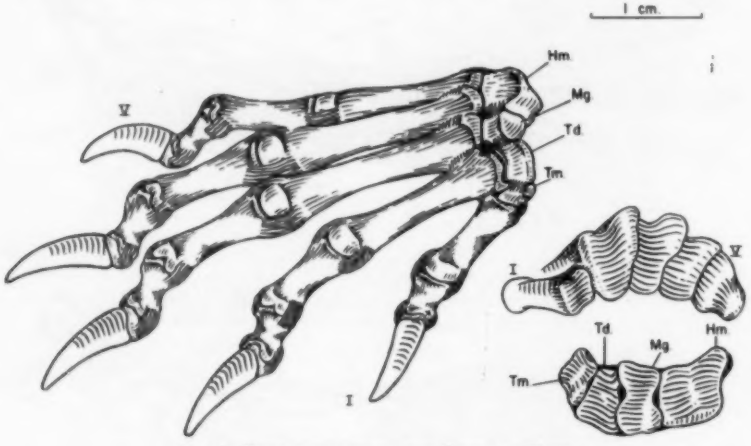

FIG. 5. *HERPESTES ICHNEUMON*, BONES OF HAND
A, digits and distal carpal bones; B, proximal surfaces of metacarpals; C, distal surfaces of distal carpal bones.

palmar pads are arranged in three pairs, with the thenar and hypothenar most proximal, the first and fourth interdigital pads intermediate, and the second and third most distal (Fig. 1, C). This may well be the primitive arrangement in mammals, as it certainly is in the Insectivora (Haines, 1955). In Carnivora the six pads may remain distinct, as in *Nandinia* (Fig. 1, D), *Galidea* (Carlsson, 1910), *Arctogalidea* (Pocock, 1915), and *Crossarchus* (Pocock, 1916), but the hand is relatively wide and the interdigital pads form an arch (Fig. 7, H), an arrangement also found in the desertic marsupial *Dasycercus* (Wood Jones, 1925). In the early Carnivora they were probably similar, for the hands of *Claenodon* and other Paleocene genera described by Matthew (1937) are also wide. In *Herpestes* the pollex is somewhat reduced and set far back in the palm, and the first interdigital pad has been lost and the other three fused, though they are more distinct in the specimens figured by Carlsson (1910) and Allen (1924) than in that figured here (Fig. 1). These features are undoubtedly cursorial specializations.

In *Didelphys* the pads are striated, as in many other marsupials, mostly arboreal, and this, taken with the frequent occurrence of striation in placental mammals, might suggest that the smoothness of *Herpestes* is another cursorial feature. But in other marsupials, including arboreal forms such as *Trichosurus* (Pocock, 1921b), the pads are tuberculated rather than striated (Fig. 7, A), and though Huxley's postulate of a common arboreal ancestor for marsupials can hardly be questioned, it is by no means certain that that ancestor had striated pads. Gregory (1920), Le Gros Clark (1924), and others have emphasized the similarity among placentals between tupaiid insectivores and lemurs, and Simpson (1945) included both groups

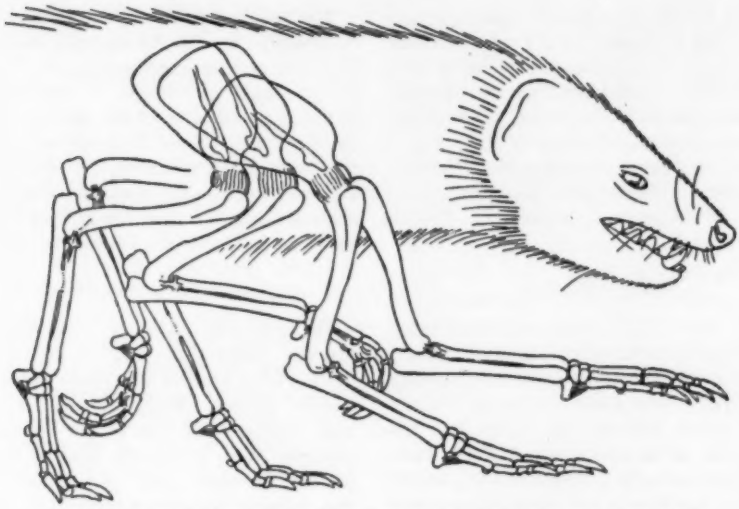

FIG. 6. *HERPESTES ICHNEUMON*, MOVEMENTS OF THE FORE-LIMB IN A SLOW WALK

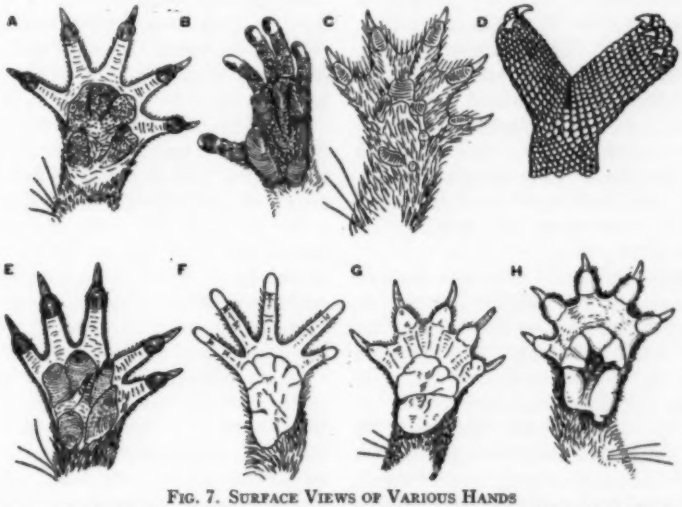

FIG. 7. SURFACE VIEWS OF VARIOUS HANDS

A, *Trichosurus vulpecula* (Pocock, 1921b). B, *Lemur niger* (Murie & Mivart, 1872). C, *Mustela vison* (Pocock, 1925a). D, *Chamaeleon vulgaris* (original). E, *Phalanger maculatus* (Pocock, 1921b). F, *Chiropotes albinasa* (Pocock, 1925b). G, *Tayra barbara* (Pocock, 1921a). H, *Arctogalidea trivirgata* (Pocock, 1915).

in his Lemuriformes. But Haines (1955) found that they have different and therefore independent types of arboreal specialization, and that the smooth-padded shrew *Crocidura*, rather than forms with striated pads, represents the most primitive arrangement among Insectivora. Pocock (1921a) found that among Carnivora *Tayra* and *Grison*, the one a tree-climber and the other a ground-hunter, the most primitive of the Mustelidae, both have smooth pads (Fig. 7, G), while the more advanced types *Martes* and *Mustela*, the one a "prodigious jumper" and the other terrestrial, both have striated pads (Fig. 7, C). Whipple (1904), after a detailed examination of the minute struc-

ture of the striations, suggested that they have been developed independently at least in the marsupials, rodents, and primates; and it seems likely that in carnivores too, where they are restricted to the Mustelidae and Procyonidae (*Potos*, Kidd, (1907), and are inconstant even there, they have arisen independently as secondary specializations. At least their distribution gives no support to the suggestion of an arboreal ancestry for the placentals as a whole.

Extensor Muscles

Herpestes has the full set of mammalian extensors found in such forms as *Didelphys* (Haines, 1939; Straus, 1942a), with no particular specializations that can be correlated with its mode of life. Matthew (1904) believed the "anomalous" arrangement of the muscles inserted on the mammalian pollex explicable if the digit was "primarily opposable," but "quite inexplicable otherwise." Gidley (1919) objected that a similar arrangement is found in *Sphenodon*, a reptile whose pollex is not opposable, but Matthew (1937) found this argument "unconvincing." Neither author specified what the peculiarities under discussion were, but they presumably include the absence of a tendon from the extensor digitorum communis to the pollex, though it supplies the other four digits; the insertion of the extensor carpi radialis on metacarpals II and III, omitting I; and the insertion of a specialized muscle of the deep layer, the abductor pollicis longus, on I.

In amphibians and reptiles there is no extensor digitorum communis; the corresponding muscle, the humerodorsalis, inserts on the bases of the metacarpals, while the terminal phalanges are extended by the dorsometacarpales and short muscles of the deep layer (Haines, 1939). In the turtle *Emys* the humerodorsalis reaches all the metacarpals, but in both amphibians and reptiles the tendons to the marginal bones may be absent, that to metacarpal V, for example, in *Sphenodon* and that to I and V in the lizard *Varanus*. In mammals the insertions are continued to the terminal phalanges, in monotremes to all five digits, while in marsupials and placentals that to I is lost except as an occasional anomaly (Straus, 1942a), but there is no reason to associate this loss with an emancipation of the pollex from participation in the movements of the other digits, for the pollex is already provided in reptiles with a full set of powerful muscles.

The abductor pollicis of mammals is identical in arrangement with the supinator manus of reptiles. The extensor carpi radialis, often subdivided into a longus and brevis, is probably derived from the reptilian extensor radialis superficialis by distal migration of its insertions from carpus to metacarpus. The insertions of the extensors of the radial digits are arranged similarly in reptiles and mammals, and the evidence from the extensor muscles supports Gidley rather than Matthew.

Flexor Muscles

The epitrochleo-anconeus is of "variable and irregular mammalian distribution," and "data relative to its absence or presence are not always reliable" (Straus, 1942a), but it may be associated with rocking of the ulna on the humerus during pronation and supination (Haines, 1950). Its presence in most primitive mammals suggests that forearm movements occurred in their early ancestors, as does also the presence of a pronator quadratus and profundus and a supinator, all inserted on the forearm bones; but the occurrence of such movements cannot be taken as evidence of arboreal ancestry, for it is only the most specialized of cursorial mammals that have lost them.

The flexor digitorum profundus is found in reptiles and mammals, giving a large common tendon that splits to supply all five digits. A distinct flexor pollicis longus has separated off in only a few mammals that have specialized types of pollical movement (Straus, 1942a). The failure of separation in Old World monkeys and in marsupials even when the pollex is opposable suggests recent development of opposition rather than its loss during the evolution of mammals.

Recent work has emphasized the close similarity of the reptilian and mammalian flexor muscles. Whereas Straus (1946) still voiced the general opinion in stating that "muscular homologies, at least between vertebrate classes, cannot be reasonably extended beyond comparison of entire palmar layers," it has now proved possible to trace each individual muscle to its reptilian source (Haines, 1950). Some small slips have been lost but no new muscles have appeared. The flexor digitorum sublimis, once thought to be a new mammalian muscle, is well developed in the palm of reptiles, whence it has migrated about half way up the forearm in carnivores and tupaiids (Haines, 1954), and this is the most striking change. There is certainly nothing to suggest any

profound alteration such as the development of a prehensile hand might be expected to bring about.

Forearm Movements

In *Herpestes* the mechanism resembles that in *Felis* and *Sciurus*, where an annular ligament has again been developed, though this is believed to be a specialization, inasmuch as the ligament is absent in *Didelphys* and *Dasyurus* (Parsons, 1900; Haines, 1946). It is at least clear that good forearm movements are not necessarily absent in terrestrial mammals, and that an oval rather than a round head to the radius need not preclude such movements. They are lost in mammals such as *Oryctolagus*, whose forearms are placed permanently in pronation as an extreme cursorial specialization, but their presence in such forms as *Herpestes* does not, as Matthew (1904, 1937) suggested, imply an arboreal ancestry for placentals.

Movements of the Pollex

Matthew's claim that the pollex of the early placentals was opposable rested chiefly on conditions in *Claenodon*, an early creodont. The drawings (Fig. 8, A–C) are made from casts of the specimens he used, the metacarpal from *C. corrugatus* being drawn at a higher magnification than the trapezium of *C. ferox*, to compensate for the difference in size between the two species.

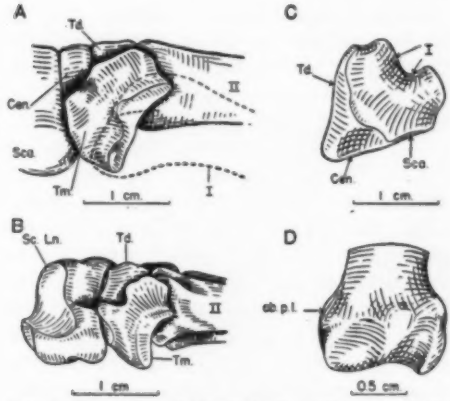

FIG. 8. FIRST CARPO-METACARPAL ARTICULATION OF *CLAENODON* AND *VIVERRA*

A, Trapezium of *Claenodon ferox* (A.M. 3269), and related bones. *B*, *Viverra civetta*, bones in radial view. C, *Claenodon ferox* (A.M. 3269), trapezium in dorsal view. D, *Claenodon corrugatus* (A.M. 16543), base of first metacarpal in dorsal view.

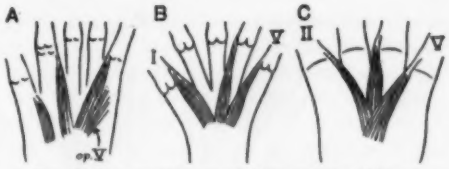

FIG. 9. CONTRAHENTES OF CONVERGENT HANDS

A, *Felis leo* (Scharlau, 1925). B, *Centetes ecaudatus* (Dobson, 1882–90). C, *Tapirus indicus* (Murie, 1871).

The trapezium has an area for metacarpal II and distinct facets for the trapezoid, centrale, and scaphoid, the area for the centrale facing obliquely dorsally and suggesting that, as in many other animals, the centrale was better developed on the dorsal than on the palmar surface of the carpus. The facet for metacarpal I faces distally, radially, and palmarward and is concave, with a deep notch on its dorsal border. The articular surface on the metacarpal is placed on its proximal and dorsal surface, and is wide with an obliquely placed shallow ridge for the hollow of the trapezium. Matthew (1937) spoke of the possibility of rotation of the trapezium and flexion of the metacarpal to a right angle, but no evidence has been found for the rotation and a plasticine model of the metacarpal, prepared by reversing and enlarging the cast from *C. corrugatus*, cannot be so flexed on the trapezium of *C. ferox* without dislocation. The whole mechanism appears to resemble that in *Viverra* (Fig. 8, D), where the trapezium again has an elongated concave facet, though with no dorsal notch. *Herpestes* has saddle-shaped facets (Fig. 5), possibly associated with the use of the pollex as a toilet digit.

Again Matthew (1937) described the hand in the creodonts as more prehensile than the foot, a most unusual condition found only in such forms as baboons and man, where the pollex has remained opposable while the hallux has lost opposability as the foot has become readapted to terrestrial progression, or in animals such as the rodent *Coendou* (Kidd, 1904) or the carnivore *Ailuropoda* (Wood Jones, 1939), where the hand has become prehensile in association with special feeding habits. A slightly or doubtfully opposable pollex may be associated with a highly opposable hallux as in *Trichosurus*, *Hemigalago*, and *Tarsius*, and a non-opposable pollex is often found with such a foot, as in *Didelphys* (Figs. 10, A; 13, C) and *Dasyurus*. It is most unlikely that the early placentals, if they had been climbers, would have reversed the usual order of specialization. When

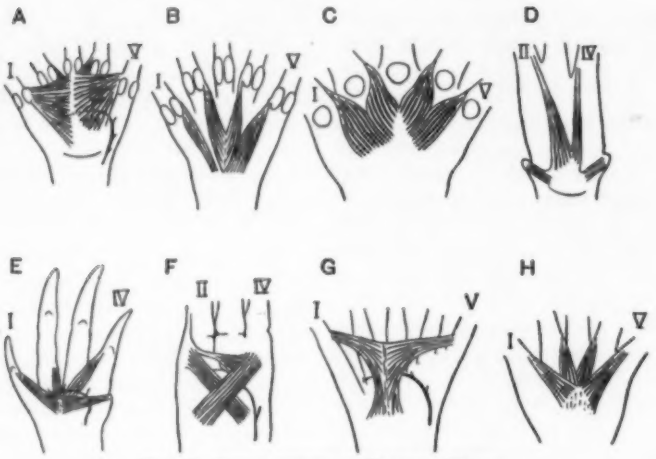

FIG. 10. CONTRAHENTES OF CLASPING HANDS

A, *Didelphys virginiana* (Young, 1880). B, *Thylacinus cynocephalus* (Cunningham, 1882). C, *Halmaturus ualabatus* (Young, 1880). D, *Perameles anurus* (Kajava, 1910). E, *Tatusia novemcincta* (Forster, 1916). F, *Bradypus tridactylus* (Cunningham, 1882). G, *Pteropus*, foot (Cunningham, 1882). H, *Dasyurus viverrinus* (Kajava, 1910).

placental climbers do in fact appear in the fossil record, as *Notharctus* in the Eocene (Gregory, 1920), the limb structure is of the usual prehensile pattern and leaves no doubt as to their habitat.

TYPES OF HAND

Convergent hands. In *Herpestes*, when the digits are flexed over the palm, they converge so that the tips lie close together (Fig. 1). This is due to the arrangement of the metacarpo-phalangeal joints (Fig. 5) so that the marginal digits face toward the center of the palm and flex over it, as do the four ulnar digits in the human hand when they are flexed (Shiino, 1925). Such a hand in which all the digits come together on flexion but diverge on extension was called a "divergent" hand by Gidley (1919), who believed this type to be primitive for placentals, as contrasted with hands that do not converge on flexion or hands with opposable thumbs. Convergent hands are well suited to scrambling over rough ground or to digging, or when provided with sharp claws to climbing, but are not suited to very fast running, to specialized swimming, to heavy spading, or to gripping branches of trees.

Convergent hands are found in most living carnivores and rodents, in most insectivores apart from the specialized burrowers and tupaiids, and in polydactylous ungulates. Gidley's belief that such hands are primitive is supported both by their distribution and by their muscular arrangement. In particular the contrahentes, a group o- muscles particularly sensitive to changes in funcf tion, form a simple fan of completely independent slips radiating to the basal phalanges (Fig. 9), as they do in reptiles, though there some of the slips arise from the flexor digitorum profundus tendon instead of from the carpal bones only (Haines 1950).

Clasping hands. Though in *Didelphys* (Fig. 1) all six carpal pads are distinct, and although the digits are all well developed and all bear claws and the hand as a whole resembles that of an insectivore, yet the animal is in fact a slow climber relying on its capability of clasping branches securely with the whole hand rather than merely catching their surfaces with the claws. Superficially the hand appears to belong to the convergent type, but the contrahentes arise from a common raphe (Fig. 10, A), so that their fibers cross the palm more or less transversely, instead of merely fanning toward the digits. The muscles to the radial and ulnar digits are more or less symmetrically arranged, so as to give equal importance to both margins of the hand in prehension, and it is proposed to call this form of hand the "clasping" type. It is found in other marsupials such as *Dasyurus* (Fig. 10, H), and traces of a common origin for the contrahentes are still seen in *Thyla-*

cinus, *Halmaturus*, and *Perameles*, which have become secondarily cursorial (Fig. 10, B, C, D).

Clasping hands are also found in edentates, with a typical raphe in the case of *Tatusia* and a peculiar crossed pattern in *Bradypus* (Fig. 10, E, F). In the walrus (*Odobenus*) a hand with a raphe serves to carry up food and stones from the sea bottom and in the flying fox *Pteropus* (Fig. 10, G) a foot with a similar arrangement hangs the animal from trees as it rests (Cunningham, 1882).

The opposable pollex. In the hands of some marsupials and primates and all lemurs the pollex is opposable. It is then more or less set off from the other digits, or at least capable of being so set off, and it must face them more or less directly. To be effective it must be strongly developed and provided with strong muscles, and indeed the degree to which the contrahens I outweighs its fellows is a most sensitive indicator of the power of opposition (Fig. 12). The thenar and first interdigital pads often approach each other and may fuse (Figs. 7, B; 11), the fourth digit may be especially elongated to act as the main opposor of the pollex, and the nail and claw may be more flattened on the pollex than on the other digits. These are all inconstant features, but may serve as useful criteria of opposability when the state of the muscles is unknown.

Wood Jones (1929) has discussed opposability very fully, emphasizing the necessity of rotation of the first metacarpal about its own long axis as an essential feature of opposition. The human metacarpal does in fact rotate through about 60° as it is drawn across the palm, the bony facets, muscles, and ligaments being so arranged as to produce this motion. When the pollex is moved back so as to lie alongside the other digits, the movement of reposition, the rotation is undone (Haines, 1944). Similar movements are found in many primates, and in the gibbon *Hylobates* a special pocket receives the pollex during brachiation (Pocock, 1925c). But the pollex may be set so far away from the other digits and in such a position that movements of simple flexion without any rotation will bring it into opposition, as in the pincer-like hand of *Nycticebus* (Fig. 12, C). Again, Pocock (1918) describes the pollex of *Chiromys* as "so long that when turned forward it overlaps the palm as in man." He did not consider it opposable, but it may be justifiable to do so if the muscles are as specialized as the thickened pollex and elongated fourth digit would suggest.

Among marsupials opposability is found only in some Phalangeridae, including *Petaurus* (Fig. 11) and *Dromicia*, where the hallux carries a flat nail (Wood Jones, 1925). Possibly *Trichosurus* belongs here, for though Pocock (1921b) found the digits "nearly evenly spaced" and the pollex "not opposable but closing obliquely backwards and inwards across the sole (palm)", and Cunningham

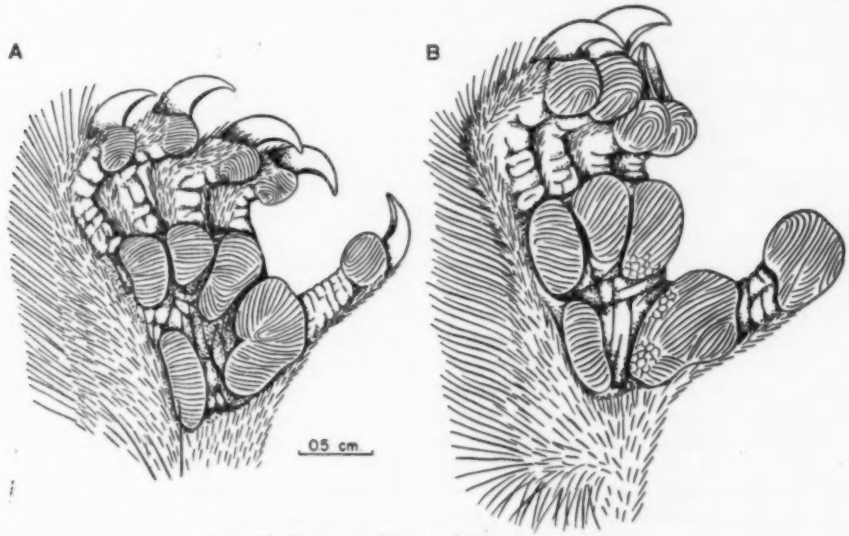

FIG. 11. HAND AND FOOT OF *PETAURUS BREVICEPS*

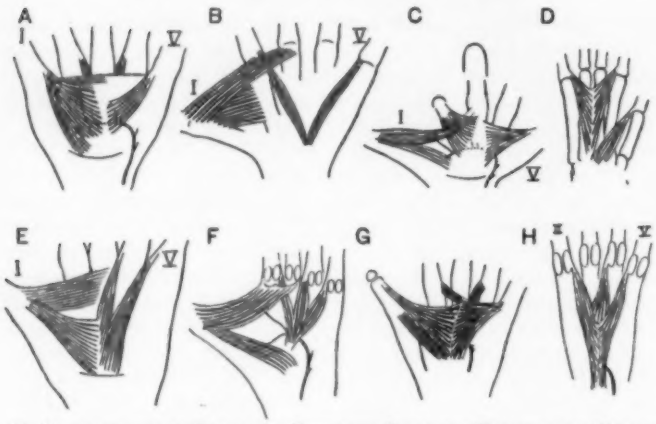

FIG. 12. CONTRAHENTES OF HANDS AND FEET WITH OPPOSABLE POLLICES AND HALLUCES

A, *Cebus fatuellus* (Forster, 1916). B, *Galago crassicaudatus* (Murie & Mivart, 1872). C, *Perodicticus potto* (Forster, 1916). D, *Ptilocercus lowii*, foot (Le Gros Clark, 1926). E, *Papio maimon*, hand (Bischoff, 1870, in Forster, 1916). F, *Cebus apella*, foot (Ruge, 1878). G, *Didelphys cancrivorus*, foot (Ruge, 1878). H, *Thylacinus cynocephalus*, foot (Cunningham, 1882).

(1882) found the contrahentes "feeble," Wood Jones described it as "alone opposable to the remaining digits," and there are but five carpal pads. Opposability is usual in the foot of marsupials except in specialized cursorial types.

Among lemurs *Hemigalago* has six pads, giving a "primitive stamp to the hand" and recalling those of "rodents, insectivores and marsupials," while the pollex is but slightly set off from the other digits (Pocock, 1918). The muscles are unknown, but in *Galago* where the pads are more flattened, as is usual in animals with strong opposition, the thenar and first interdigital pads have become approximated and in some species supernumerary pads have developed (Whipple, 1904), and the muscles are strongly asymmetrical (Fig. 12, B). In extremely specialized types such as *Perodicticus* and *Nycticebus*, the contrahentes reach a high degree of asymmetry (Fig. 12, C) and even the long flexor tendons become rearranged (Straus, 1942b).

In *Tarsius* the pollex is said to be smaller than in any lemur, closer to the second digit and not opposable (Pocock, 1918). Woollard (1925) found the contrahentes I and V similar and both arising from a raphe, and Le Gros Clark (1924a) found the movements clumsy compared with those of *Nycticebus*. On the other hand, the first interdigital and thenar pads have come into contact, and opposition in the hallux is marked, but without further information as to the musculature *Tarsius* can be included only tentatively among animals with an opposable pollex.

In the New World *Cebus* the pollex is not clearly set off from the other digits and is not usually considered opposable (Pocock, 1925b; Wood Jones, 1929), but Gregory (1920) quotes Belt on the ability to extract a cork from a bottle as evidence of gripping. Here an examination of the contrahentes (Fig. 12, A) leaves no doubt as to the presence of opposability, for they are grossly asymmetrical as they are in Old World monkeys (Fig. 12, E).

Le Gros Clark's (1926, 1927) beautiful photographs of the living *Ptilocercus* and *Tupaia* showed, he believed, a definite tendency to opposability, and he observed a *Tupaia* lifting an insect to its mouth with one hand. Both the first and fifth digits can diverge widely, so that they come to lie nearly in the same straight line. Reconstructions of the muscles (Haines, 1955) show the contrahentes II and V arising from a common raphe, forming a strong clasping mechanism for this part of the hand, but contrahens I is independent of this raphe, and forms a small muscle controlling the pollex alone. A similar condition is found in the foot (Fig. 12, D).

A reconstruction of the trapezium (Fig. 13, A) shows it articulating with the scaphoid, centrale, and trapezoid. It is closely attached by ligaments to the second metacarpal, and receives some of the fibers of the abductor pollicis longus, as stated by

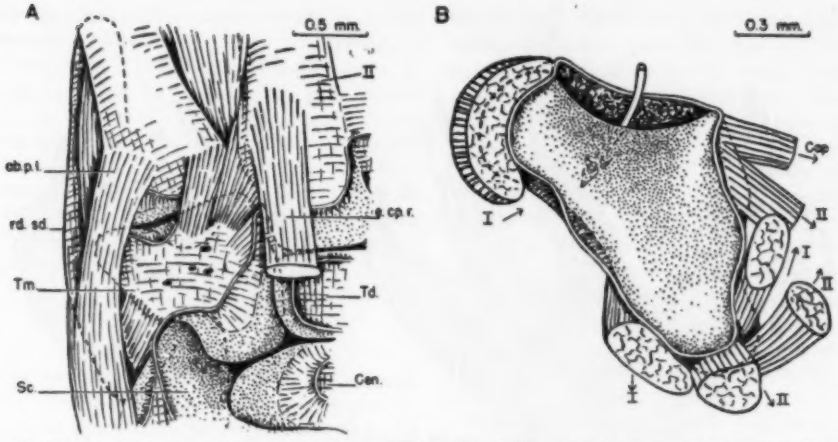

FIG. 13. *PTILOCERCUS LOWII*, RECONSTRUCTIONS OF FIRST CARPO-METACARPAL JOINT FROM SERIAL SECTIONS (RIGHT SIDE)

A, Bones and ligaments, dorsal aspect. B, Distal surface of trapezium.

Straus (1942a). The articular surface for the first metacarpal is saddle-shaped, and both the articular cartilage and the synovial cavity are continuous with those for the scaphoid (Fig. 13, B, arrow). This suggests a specialization of pollical movement superimposed on the clasping type of hand, a peculiar arrangement quite different from that of other hands with the opposable pollices and difficult to classify.

Schizodactylous hands. In the chameleons, the only reptiles with markedly prehensile hands and feet, the first three digits oppose the other two in the hand, and the first two the other three in the foot (Fig. 7, D). In the marsupials *Phalanger*, *Pseudochirus* (Fig. 14), and very markedly in *Phascolarctos* (Pocock, 1921b; Wood Jones, 1925) the first and second digits oppose the others, and a similar arrangement has developed independently in the New World monkeys *Cacajao*, *Lagothrix*, *Alouatta*, and *Chiropotes* (Pocock, 1920, 1925b: "zygodactylous" hands). Well-developed contrahentes pass to both radial digits (Fig. 15).

Schizodactylous hands may have developed either from the simple clasping type, or from those with an opposable pollex. It would appear at first sight impossible for the second digit to cross the gap so as to align itself with the pollex instead of with the other digits, and it is tempting to suggest that the common ancestors of animals with the two kinds of gap can have had no gap at all, implying that their hands were of the simple clasping type. But whereas in the feet of most birds the hallux opposes digits II, III, and IV, V being lost, in several groups the digits are divided two and two (Evans, 1899). This is usually due to a turning back of IV, so that I and IV oppose II and III, as in cuckoos (Cuculidae) and parrots (Psittacidae); but in the trogons (Trogonidae) it is II that turns back to join I, so crossing the gap and giving a foot comparable to the schizodactylous hands of mammals. Since also in both marsupials and primates schizodactyly and opposability of the pollex are found in closely related genera and since such features as fusion of pads and elongation of digit IV are found in both types, it is reasonable, though by no means necessary, to regard schizodactylous hands as a further development of those with an opposable pollex.

Loss of opposition. Gregory (1920), Wood Jones (1927), and others have distinguished between slow careful climbers, such as *Didelphys*, and acrobatic climbers that leap over or brachiate under the branches. The pollex is not essential to acrobatic climbers, but may be retained for feeding; or, alternatively, it may be dwarfed or lost as in *Ateles* among New World or *Colobus* among Old World forms (Straus, 1942b). Again, in the gelada baboon (*Theropithecus*), which has abandoned arboreal life and become secondarily cursorial, the pollex has become reapproximated to the other digits (Pocock, 1925c), while in the pes of *Thylacinus* and some other marsupials the hallux has been lost (Fig. 12, H). Possibly the unique arrangement in the American marsupial *Caeno-*

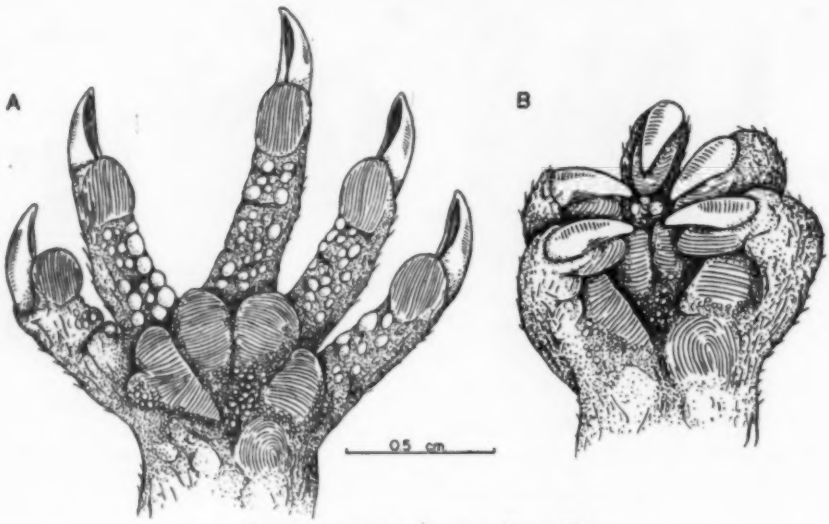

FIG. 14. *PSEUDOCHIRUS CONVOLUTOR*, POUCH YOUNG

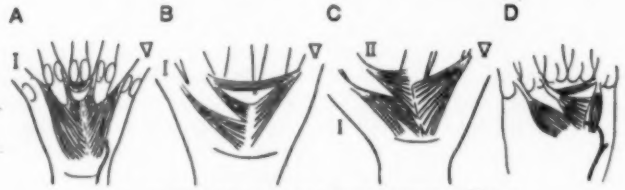

FIG. 15. THE MUSCLES OF SCHIZODACTYLOUS HANDS

A, *Phalanger maculatus* (Cunningham, 1882). B, *Phalanger orientalis* (Kajava, 1910). C, *Phascolarctos cinereus* (Kajava, 1910). D, *Tamandua tridactyla*, foot (Cunningham, 1882).

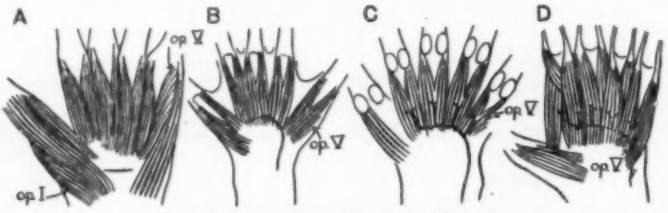

FIG. 16. EXAMPLES OF OPPONENS MUSCLES

A, *Papio maimon* (Bischoff, 1870, in Forster, 1916). B, *Didelphys cancrivorus* (Kajava, 1910). C, *Dasyurus maugei* (Forster, 1916). D, *Pan troglodytes* (Forster, 1916).

lestes, in which both pollex and minimus have nails but the other digits claws (Osgood, 1921), may indicate former opposability of both these marginal digits, but the genus is too isolated for certainty.

The opponens muscles. Wood Jones (1927) suggested that opposition is "produced by the correlated pull of several muscles of which the opponens pollicis was the most important." If by opponens muscles are understood short hand muscles inserted into the shafts of the metacarpal bones, these, as Cunningham (1882) stated, may be of two kinds. In most carnivores there is an opponens V lying on the palmar surface of the deep ulnar nerve, derived from a part of the contrahens V whose insertion has migrated proximally from the basal phalanx as in *Herpestes* (Fig. 3, C),

while in marsupials a similar muscle is derived from the ulnar head of the flexor brevis profundus V (Fig. 15, B, C). In primates there may be an opponens I and an opponens V, both derived from the flexores breves profundi (Fig. 16, A, D). Since the opponens V is widely distributed though there is no opposition in the minimus, and since marsupials and lemurs may have opposition in the pollex without the development of an opponens I, the muscles cannot be of any particular importance for the movement.

DISCUSSION

Specialization of the hand

The forearm and hand of the Egyptian mongoose, *Herpestes ichneumon*, a terrestrial carnivore, have been described in full anatomical detail, and some of the mechanisms of the joints and muscles have been discussed. After comparison with the corresponding parts of other animals, it has been suggested that this hand is close to the primitive mammalian type, though it does show a few specializations of its own, associated with a cursorial habit. As the general arrangement of the bones is similar to those found in the earliest placentals whose hand skeletons are known, it has been suggested that these too were terrestrial animals, able to walk, run, scramble, leap, dig, and swim, and that they were not in the habit of climbing trees.

On the other hand, the view that the early mammals were arboreal has led to a search for structural peculiarities associated with this habit. By using a combination of surface features, muscle arrangements and bone and joint forms, the various types encountered can be distinguished more clearly than is otherwise possible. Thus several authors have cited the hand of the common opossum, *Didelphys virginiana*, a slow, careful climber, as of primitive type, as indeed it is in general shape, disposition of digits, arrangement of carpal pads, and form of the claws. But the arrangement of the muscles places it in the "clasping" type, in which the contrahens muscles to digits I and V arise from a common raphe and cross the palm transversely to form a special mechanism for drawing the marginal digits together. In *Herpestes*, on the contrary, though the digits are so articulated that they fall together as they are closed over the palm, giving a "convergent" type of hand, the contrahentes form a simple fan, with no specialization of the slips to the marginal digits. Since convergent hands are widespread among placentals, and the reptilian muscles corresponding to the contrahentes are arranged in a fan, it is suggested that the clasping type is derived from the convergent, and not vice versa.

The rearrangement of the muscles leads the way to the more specialized prehensile types of hand, those in which the pollex is opposed to the remaining digits during grasping, and schizodactylous hands in which the first two digits are opposed to the other three. In these the muscles become highly asymmetrical, with great development of the slips to the opposable digits, but the arrangements are clearly derived from those of the clasping type.

Readaptation to a terrestrial habit is found in many marsupials and primates, but in each case the hand preserves the arboreal adaptations in recognizable form, whether the readapted hand is derived from a simple clasping type as in terrestrial marsupials, or a more advanced type as in the baboons and man.

It remains to consider some other features that have been quoted in support of an arboreal ancestry for mammals as a whole, particularly feet, body proportions, and prehensile tails, and the behavior of arboreal animals.

The arboreal foot

In all animals specialized for climbing the foot is at least as advanced as the hand, and usually more so. Whereas in *Didelphys* the hand is of a simple clasping type with symmetrically placed digits and contrahentes, the foot has a large opposable hallux, set off from the other digits and provided with a special musculature. In the monkey, *Cebus*, there has been some doubt among naturalists as to the opposability of the pollex, which is not clearly set off from the other digits, but in the foot the hallux is set well away from the other digits. It is only in the most specialized climbers, such as the koala *Phascolarctos* or the potto *Perodicticus*, that specialization of the hand catches up with that of the foot.

When arboreal animals become readapted to terrestrial life the less specialized hand may be little changed, while the more specialized foot requires more profound alteration. This is well seen in man, where the hand is of typical primate type while the foot is unique in possessing a great toe that has lost all power of opposition. Again, in

many terrestrial marsupials the hand retains a simple clasping structure, while in the foot the once prehensile hallux has been reduced to a toilet digit or discarded altogether.

Schizodactylous feet, found in chameleons, are unknown in mammals, but convergent and clasping feet, and feet with the hallux fully opposable, resemble the similar types of hands. The beautiful series of figures published by Ruge (1878) again shows fanned, symmetrically transverse, and asymmetrical arrangements of the contrahentes, and a detailed study of the feet would doubtless lead to the same conclusions as those from the hands. Where the bony structure of the foot is known in early placentals (Matthew, 1937), it is even less suggestive of arboreal habits than in the hand.

Prehensile tails and body proportions

Prehensile tails are found in some fishes (*Hippocampus*), but are usually associated with climbing, the only known exception being the rat-kangaroo (*Bettongia*), which uses its tail in collecting sticks and grass for nest-making. Prehensility varies from a tendency to press against or coil spirally around a support, as in many mice, through a systematic coiling around stems, as in the harvest mouse or the nectar-eating marsupial *Tarsipes*, to the ability to support the whole or the greater part of the body weight by the end of the tail alone placed squarely across a branch, as in the opossums and spider monkeys.

When fully prehensile the tail is long, and rather thick even toward its tip. The contact surface is hairless and may be crossed by a complex series of papillary ridges. The vertebrae are well developed and provided with strong processes, and near the tip they may be short and wide, so as to resemble the phalanges of a digit. The musculature may be stronger than usual, but is not especially differentiated, for in all well-developed tails the long and short muscular slips attached by tendons on either side of each dorsal and ventral spine and transverse process are adequate for carrying out all possible movements.

Prehensile tails are found in many marsupials, the tree porcupines and anteaters, the carnivores *Arctictis* and *Potos*, and in several genera of New World monkeys. But even in some of these animals it would be difficult to say, from the bones alone, that the tail was prehensile and the animal arboreal, and in animals that merely use the tail to press against or twine around branches it would not be possible. The claim made by Matthew (1937) for the prehensility or semi-prehensility of the tails of early mammals on osteological grounds cannot be justified. Indeed *Herpestes*, which uses the mass of its heavy tail to fling itself from side to side as it attacks, and to turn its body when it is dropped back downward, has the caudal vertebrae as heavily built as many fully prehensile forms.

Again there is nothing distinctive in the body proportions of arboreal animals. Matthew (1937) compared the proportions of early mammals such as *Claenodon* and *Loxolophus* with *Potos*, in which the tail is as long as head and body together, and with *Paradoxurus*, which shares with *Potos* the rare ability to climb down a tree head first (Hodgson, 1847). But even longer tails may be found in the terrestrial *Linsang* or *Genetta* (Allen, 1924).

Acrobatic climbers from slow climbers

When acrobatic climbers develop from relatively slow-climbing stocks they may show additional peculiarities superimposed on the original specializations. Thus the South American monkey *Callicebus*, a "fairly slow-moving, non-prehensile-tailed climber," may be taken to have preserved an early type of primate locomotion (Hill, 1956). Here the external features of the hand are of the simple prehensile type of *Cebus*, in which, however, the tail has also become prehensile. In *Cebus* the pollex is moderate in size, but is provided with a well-developed and asymmetrical adductor musculature. But in the spider monkeys *Ateles* and *Brachyteles* the pollex is reduced or lost, and the musculature usually "rudimentary" (Straus, 1942b). The atrophy is associated with the use of the hand as a hook from which the animal hangs by its long arms as it swings from branch to branch in brachiation, a use in which the pollex could play no part.

In the marmosets (Hapalidae), a group of small New World monkeys that run and leap over branches like squirrels, the digits have sharp claws instead of the nails found in most primates, and the pollex has become realigned with the other digits. The changes are believed to be secondary adaptations (Gregory, 1920) associated with a peculiar gait.

The pollex is reduced in several genera of Old World monkeys and is absent in *Colobus* (Straus, 1942b) again in association with running and

leaping habits. In the great anthropoid apes it is not actually reduced, but has been left behind by the elongation of the other digits, and the muscles are relatively poorly developed, while in the gibbons it can be accommodated temporarily alongside the metatarsals of the other digits so as to be out of the way in brachiation.

In these forms that practice acrobatic climbing there is, then, in each case, a mechanism for disposing of the pollex during fast locomotion, and the divergence of the methods by which this is done in different groups gives strong support to Hill's (1956) thesis that all primates are derived from a slow-climbing, grasping stock. A similar arboreal stock must have given rise to the lemurs, among which the most extreme specializations are found in the very slow climbers, *Nycticebus* and *Perodicticus* (Straus, 1942b). The pollex and fourth digit are enlarged to form a pincers mechanism, the pollex being placed permanently in a position of opposition with no possibility of reposition alongside the other digits, while the second and to some extent the third digits are reduced.

Acrobatic climbers from terrestrial scramblers

Among the primates acrobatic climbing is always associated with structural specializations of the limbs, but in the arboreal carnivores there are remarkably few such changes. Thus the Indian mongoose *Herpestes mungo* is an accomplished climber, and takes readily to the trees, but is structurally very similar to the terrestrial *H. ichneumon*. The pine marten, *Martes martes*, can run down a squirrel leaping through the canopy and walk down a trunk head first, yet its hands and feet show little difference from the terrestrial polecat *Mustela putorius* or the semi-aquatic mink *M. vison* (Pocock 1925a). In fact, the striated pads of *Mustela* would appear better adapted to arboreal life than the papillated pads of *Martes*. Pocock (1921c) found *Tayra* and *Grison*, the one an "active tree climber," the other an "agile ground hunter," similar in limb structure, so that their habits could not be diagnosed were only fossil material available.

It is possible, then, that some of the early carnivores supposed by Matthew to have been arboreal may indeed have been so, but there is no skeletal evidence such as he claims for this, nor should any be expected. Small agile animals used to running or scrambling over rough surfaces can take to similar modes of progression in trees by changes in behavior without profound changes in limb structure. The claws of such acrobatic climbers may be rather sharper than those of their terrestrial relatives, as in *Martes*, *Paradoxurus*, or *Ailurus*, and the animals may fight on their backs, using all four feet at once. But clasping or prehensile hands are not found among carnivores, and those that use the hand in feeding, the raccoons, coatis, and bears (Hodgson, 1847), though they all climb, are not highly specialized for arboreal life.

It is difficult to decide how the arboreal rodents originated. Matthew (1910) reconstructed the Eocene ischyromyid *Paramys* as a squirrel-like animal with a bushy tail, and suggested that it was arboreal. In many rodents (Muridae, Sciuridae, etc.) the reduced pollex carries a nail, and the contrahentes pass somewhat transversely from a "common palmar tendon" (Rinker, 1954) somewhat similar to that of the insectivores (Haines, 1955), but in the rodent foot the hallux is usually unmodified. Unfortunately, no great body of information about the hand of rodents is available in the literature, and the question of their origin must be left open.

Reasons for tree climbing

A few specialized arboreal mammal-eating predators have been developed, including snakes, monkey-eating eagles, and several carnivores, but on the whole arboreal animals are less subject to predation than terrestrial forms. Many are relatively unarmed, and depend on inconspicuousness (sloths), unpalatability (koala), or rapid escape (squirrels and monkeys). Some animals (cats and bears) climb trees when hard pressed on the ground, even though on descending they can only scramble down clumsily backwards.

Hollows in trees give good protection and are extensively used for resting (squirrels, opossums), sometimes by animals that normally hunt on the ground (*Bassariscus*), though the opposite habit, tree-feeding and resting in burrows, is more usual (*Procyon*, *Mungos*).

Most climbing is for food. Arboreal marsupials, carnivores, and primates will usually take any small animals, vertebrate or invertebrate, young birds or eggs that may be available. A number climb for leaves, and these include many of the most specialized types, that seldom come down to the ground (koala, sloths). Where fodder is scarce animals from unexpected groups may become arboreal, such as the tree kangaroos,

porcupines, and hyraxes. In North Africa domestic goats are becoming pests of fully grown fruit trees, for they have learned to climb on high branches and browse off the foliage.

Nectar-feeding is particularly well developed in Australia (*Dromicia*, *Tarsipes*), but is profitable only for relatively small animals. Larger forms may raid the nests of social insects, termites, ants, wasps, or bees. Fruit-eating is widespread, even among animals usually carnivorous such as mongooses and foxes, and arboreal forms may pluck the fruit before it drops. Monkeys and civets may, in some forests, be as important in seed-distribution as birds or fruit-eating bats, and several fruits, such as mangoes, are particularly well suited to attract and be disseminated by climbing mammals, and appear to have been developed in symbiosis with them (Ridley, 1930).

The Cretaceous forests and the habitat of early placentals

The early Cretaceous forests included few or no flowering plants (angiosperms), but were made up of tree-ferns, pteridophytes, cycads, and conifers in great variety. Now, judging from modern examples, non-angiospermous trees are singularly unpalatable. They are usually avoided not only by most browsing mammals but also by insects, apart from a few specialized types, and their leaves or fronds are usually seen intact, however much the neighboring angiospermous foliage has been eaten. Fossil ferns and cycads are also usually found uneaten.

Nectar was not available, for insect pollination is not the rule except in angiosperms, and the enormous population of nectar-seeking insects found in modern forests had not yet developed. Nor were caterpillars, grubs, or honeycombs available as food. Again, though a few conifers (*Taxus*) have developed fleshy edible fruits, these are specialized and probably relatively modern types, and related to avian rather than mammalian consumption.

Taken as a whole, then, these early forests would not offer much scope for arboreal life. Possibly ground-living mammals might climb trees to escape predators or seek rest, and it has been suggested that, since the dinosaurs dominated the ground level, the early placentals of the forests had to live in trees to escape them. But there was probably plenty of undergrowth and floor debris to accommodate the small insectivorous forms that are the only placentals known to have existed at that time. The multituberculates actually lived with and eventually survived the dinosaurs, and nobody has suggested that they were ever arboreal.

With the sudden advent of angiosperms and their revolutionary effects on the insect and avian populations of the forests, possibilities of arboreal specialization opened for the mammals. Marsupials lived in Upper Cretaceous times, and though their limb structure is unknown, they were probably the earliest arboreal group, followed by the lemurs and primates in the Paleocene and Eocene, and other groups from time to time. This interpretation agrees with Dollo's (1889) conception of a sporadic evolution for the various arboreal types. In modern forests different species may be specialized for life at particular levels of the canopy or branches (Hill, 1956).

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SUMMARY

1. External form and internal structure allow most pentadactyl mammalian hands to be classified as *convergent*, in which the digits fall together when they are flexed on the palm; *clasping*, in which the contrahentes muscles to the marginal digits are more or less transversely arranged; hands with *opposable pollices*, in which the contrahentes muscles are asymmetrical; *schizodactylous hands*, in which two digits oppose the other three; and hands in which opposability has been lost.

2. The hand of *Herpestes ichneumon* is described as an example of a strictly terrestrial convergent type, with some cursorial adaptations. The clasping and fully prehensile types appear to have been derived from the convergent type.

3. Specializations of the hands, feet, and tail such as are characteristic of many arboreal animals, particularly of slow, deliberate climbers, cannot, so far as can be judged from the skeleton, be recognized in the earliest placental mammals.

4. In spite of the suggestion frequently made that the placental mammals as well as the

marsupials were primitively arboreal in habit, it seems more probable from the structure of the hand of *Herpestes* and a comparison between it and other types that the earliest known placentals had hands of convergent type, and like *Herpestes* were terrestrial in habit.

5. The early Cretaceous forests appear to have offered little scope for arboreal life, but since their replacement by angiospermous forests of modern type the abundance of insects and fruits available as food has led to the adoption of arboreal habits by several distinct groups of mammals.

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ON THE EVOLUTION OF THE ANIMAL PHYLA

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INTRODUCTION

THE PHYLOGENY of the animal kingdom remains a matter of perennial interest to zoologists, although it cannot be said that any new important facts bearing on phylogeny have come to light in recent years. I will avoid a discussion of the various phylogenetic hypotheses and theories extant in the literature and will limit myself to an exposition of my own views. Only articles read or reread will be cited. On all essential points in the following article I agree with the views of Remane (1954a), who has expounded the history of animals with outstanding knowledge of the paleozoologic and neozoologic facts, in many cases down to the orders. Remane's rigor in establishing homologies (1952, 1954a) is worthy of emulation. That Remane's (1954a), Ulrich's (1950), and my own opinions coincide to such a high degree is certainly owing to our common zoological descent from Karl Heider. I cannot equal Heider in wisdom, but try to remember how serenely he pondered the matter of phylogeny. The present appears to be the first presentation of this school of phylogeny in the English language.

As the oldest known fossils already belong to the same separate phyla that exist today, their predecessors must be deduced subjectively. In many phyla there are known no such useful fossils as the Trilobita, *Protobatrachus*, and *Archaeopteryx*; hence such intermediate forms must be constructed. The connections between recent classes and orders are never concrete but must be understood as an abbreviated terminology.

RELATIONSHIPS WITHIN THE PROTOZOA

The following notes on the Protozoa are compilations from the literature, as I have had little first-hand experience with this phylum; they reveal the many unsolved problems in this ancient subkingdom with its immeasurably long evolutionary history.

Plants, the holophytic Flagellata (Phytomastigina), stand at the bottom of the Animal Kingdom. Flagellates of animal nature (Zoomastigina) and other acellular and unicellular animals (Protozoa) have arisen from them along different lines. Simple animal flagellates, e.g., Protomonadina and Rhizomastigina, are related to the Chrysomonadina. The Protomonadina may be ancestral to complicated animal flagellates, such as the Polymastigina, that lead to the Hypermastigina. Comparable with the latter, although not derivable from them, are the Opalinida, a separate order of Zoomastigina. These are related to the Ciliata by their cilia and by the absence of a centrosome, an uncommon feature in higher flagellates.

Since many lower Rhizopoda are inseparable from the Flagellata, Grassé (1952) unites the Rhizopoda with the Flagellata as a subphylum, Rhizoflagellata. The Amoebina are polyphyletic and have their origin in different orders of the Phytomastigina, e.g., in the Chrysomonadina, or in the Zoomastigina, e.g., the Endamoebidae in parasitic Protomonadina. The Testacea originate partly from the Amoebina; in part show relationship to the Foraminifera; and in part descend from the Rhizochrysidae (*Chrysothylakion*), which are chrysomonads. The latter seem ancestral also to the Heliozoa, as the axopod-bearing Cyrtophorina lead to the Helioflagellidae and the Centrohelidia. A further phytomastigote order, the Dinoflagellata, is an important starting point for other Protozoa also. The gametes of Cystoflagellata (*Noctiluca*) indicate their origin from the Gymnodiniidae. Possibly the Radiolaria and Foraminifera also came from Dinoflagellata. This is suggested by their polyploid nuclei and biflagellate gametes. Hollande (1953) has recently compared peridinean and acantharian nuclei.

Among the Sporozoa, the Telosporidia are altogether derived from Zoomastigina and by some, but not all, authors, more precisely from the Bodonidea. Poisson (1953) unites the Babesi-

idae and Theileriidae as Babesioidea; these are probably Haemosporidia. Also the Sarcosporidia can be related to the Telosporidia, perhaps to the Coccidia. The Haplosporidiidae, the only animals that remain in the Haplosporidia after others have been recognized as fungi, are possibly derived from the Amoebina. The lid of the haplosporidian spore has been homologized with the thread of cnidosporidian capsules.

The young amoeboid sporoplasm that hatches from the spore of the Cnidosporidia suggests a rhizopod ancestry. The spores of some Microsporidia are possibly organelles. If this is the case, their polar capsules would recall the cnidotrichocysts of certain dinoflagellates (Gymnodiniidae: *Polykrikos*, *Nematodinium*). One could, with Chatton, compare the polar thread with a flagellum; but none of these relations brings forth a plausible indication of the origin of the Cnidosporidia. In two orders of the class the spores are organs with cystogenous and capsulogenous cells and germ-nuclei. In some species a somatic and a sporoblastic nucleus (germ-nucleus lineage) can be distinguished already in the young binucleate sporoblast. In the Cnidosporidia a perishable soma and a potentially immortal germ are separated to a higher degree than in any Protozoa (Poisson, 1953). Since Stolc, who discovered the Actinomyxidia, several authors, and recently Ulrich (1950), do not include the Cnidosporidia among the Protozoa. Cnidosporidians have even been compared with the parasitic larvae of the medusan family Cuninidae (Weill, 1939) and indeed their polar capsules agree with atrichous isorhizas. But there are clear protozoan traces in the life cycle of the Cnidosporidia because the spore begins as a zygote in the Actinomyxidia, and the caryogamy of the haploid nuclei in the sporoplasm is automixis in *Myxobolus*. Perhaps it is easier to understand the Cnidosporidia as having originated from cytomorphous Protozoa and having evolved along a blind alley on a line independent of the origin of the Metazoa.

With much more success than the Cnidosporidia, the flourishing Ciliophora have entered upon a division of labor into somatic and generative functions without subdividing the cytosome. Their nuclear dimorphism and process of conjugation separates this subphylum far from all other Protozoa. The genetics of ciliates accords with that of other Protozoa (Hyman, 1940). As ancestors among the living Protozoa, only the flagellate order Opalinida can be suggested. Some articles mentioned in Hall's (1953) list of literature evidence that, beyond the common possession of cilia, also the nuclear structure and mitosis of some *Opalina* species show features characteristic of ciliates. Furthermore, the fibrillar system of opalinids resembles that of the Holotricha. The latter, an order of Ciliata, is today considered as ancestral to the second class of Ciliophora, the Suctoria (Hyman, 1940).

POSITION OF THE MESOZOA

The so-called Mesozoa (Dicyemida and Orthonectida) are Histozoa, not stereoblastulae (Moruloidea). Their epithelial or syncytial outer layer performs the functions of protection, locomotion, and nutrition. The process by which the inner cells constitute new individuals may be called somatic parthenogenesis or polyembryony. Sexual orthonectids are structurally similar to dicyemid nematogens, and the swarmers are also similar in both orders. The orthonectid swarmer sheds its ciliated epidermis when it penetrates into the host; and thus the first parasitic stage of orthonectids is homologous with the axial cell of nematogens. The life cycle can be compared with that of digenetic trematodes in which, as in both orthonectids and dicyemids, swarmers originate from fertilized eggs. Mesozoans afford comparison with a simplified miracidium or with the male of the echiuroid *Bonellia*. The occurrence of copulation in orthonectids, with the male discharging sperm into the female genital opening, suggests that they are less primitive than the lower Metazoa (Porifera, Radiata, Archicoelomata) in which fertilization is external. Copulation first occurs in the lower Spiralia, i.e., flatworms. The self-fertilizing, hermaphroditic dicyemidan "adult," which lives inside the axial cell of a rhombogen larva (McConnaugheys, 1954), can only be understood as a very much reduced stage. I think the Mesozoa must be derived from the Digenea and are digenetic larvae with utterly reduced structure and a complicated life cycle.

ORIGIN OF THE METAZOA

The origin of the Metazoa must be traced from protozoan colonies. Such aggregations of individuals as occur in flagellates, rhizopods, and ciliates evince important parallels with ontogenetic stages of numerous Metazoa. The motor forces of the many individuals of a colony are additive; spherical colonies have relatively smaller

surface and relatively less friction than a unicellular individual (Hesse, 1935). In polarized colonies one can observe an accumulation of nutritive particles at the posterior pole (Korschelt and Heider, 1909; Heider, 1914). Here the phagocytic cells are better nourished than the cells at the anterior pole, and hence grow more rapidly. As motile animals generally place growing parts inside, a trap for food particles at the posterior end results. These ideas about coeloblastula and embolic gastrulation will maintain their place because of their high explanatory value (Remane, 1954a).

The embolic gastrula is very common in widely separated phyla (Jägersten, 1955). Epiboly is not a special type (Korschelt and Heider, 1909); it is connected with emboly by numerous transitions. Paucicellular ingression cannot be separated distinctly from the two mentioned types, and multicellular ingression at the vegetative pole can also be understood only as a secondary modification of invagination. I therefore agree with Jägersten (1955) that the common ancestor of the Metazoa possessed embolic gastrulation, i.e., was simply a gastraea (Haeckel, 1874).

From a strictly morphological viewpoint, gastrulation by invagination may appear as an embryological "short-cut" (Hyman, 1940), because an organ develops in the stage of germ-layer formation (Goette, 1921). We must, however, consider the archigastrula as a living organism. All its cells are in contact with the water and hence can easily perform respiratory and excretory functions, for the archenteral cavity is filled with outside medium (Hesse, 1929). In all cases of apolar gastrulation these functions are more difficult to accomplish. In a parenchymella (phagocytella, planuloid), respiration and excretion must be effected by diffusion. For defecation the entomeres must transmit their residues to the surface or make their way to the outside through the mass of inner cells.

Although we must imagine that the Metazoa began as protozoan colonies, the metazoan body can only be compared to a diploid cytomorphous zygote (Boettger, 1952) subdivided by continued diploid division, and not to a colony of individuals united in a ball of jelly. The vegetative phase of histozoan animals plays an ever increasing role, whereas the germ cells with their meiosis generally appear late in life. The haploid gametes are at first discharged into the surrounding water, as in Protozoa; later they become more and more protected, and diploid organs and systems serve to assure the survival of the species by ever more-complicated means. The line of the Metazoa diverges from that of the Protozoa from the beginning. The often sharp separation of soma and germ in Metazoa, combined with an always increasing preponderance of the soma, justifies the presumption that the metazoan line began later than the protozoan and that, if the conditions of life worsen, it will end earlier.

SPONGES, CNIDARIA, AND CTENOPHORA

The oldest animals, the Zoomastigina, evidently gave origin to sponges and coelenterates, which are connected at their common root (Heider, 1885). Transitory forms between flagellates and sponges do not exist, as *Proterospongia* is a regenerating fragment of a sponge (Tuzet, 1945). As sponge larvae have ordinary flagellated cells, the Porifera need not have arisen from the Choanoflagellata. In any case, sponges and Cnidaria must have originated together, because both have germ layers. There exist other parallels between sponges and true Metazoa (Eumetazoa). The definitive layers of the Calcarea and simple Tetractinellida are achieved by a process similar to gastrulation by invagination. What previously had been described as inversion of the germ layers is understood today as multipolar inwandering (Meewis, 1938). Spongillids show an "accélération embryonaire" (Brien and Meewis, 1938) like many limnic Eumatazoa. The alterations of shape in the blastula (pseudogastrula, stomoblastula, "plissement" of the coeloblastula of *Halisarca*) are intelligible as the result of the small space available for embryonic expansion in the body of the parent sponge. The evolutionary line of sponges was divergent from the beginning and ends blindly.

Flagellates with cnidotrichocysts stood at the root of the Cnidaria. We agree with Ulrich (1950), Remane (1954a), and Jägersten (1955) in reversing the sequence Hydrozoa-Scyphozoa-Anthozoa. A tetraradiate polyp (Korschelt and Heider, 1890) with four gastric pouches separated by septa may have been the ancestral cnidarian (Remane, 1954a). The gastric pockets contained the germ cells that were expelled through the mouth. The disposition of the organs around a heteropolar axis suggests a sessile ancestral form of the Coelenterata (Heider, 1914). The single aperture of the intestine favors this opinion. Where the planula

develops into a medusa, as in Trachymedusae and Narcomedusae, it passes through a stage that is at least very similar to a polyp (Korschelt, 1936); or an actinula appears that transforms into a medusa. Likewise the planula of the Siphonophora passes to a polypoid form, the first gastrozoid of the colony. The ancestral form was probably solitary like most of the Tetracorallia and had, as in Actiniaria in general, a coeloblastula and an embolic gastrula.

From this primitive stage the anthozoan polyp arose by development of an ectodermal pharynx, by increase of the number of septa, and by further complications. Among these complications, the most remarkable feature is a bilateral tendency, manifest in both larval and adult stages. Mouth and pharynx become oval or slitlike, making possible the development of one or two siphonoglyphs, sulcus, and sulculus. The so-called zoanthella-larva has very long cilia on one side of the body. The septa are biradially or bilaterally arranged. Already the precursors of the hexacorals, the Tetracorallia, which appeared in the Ordovician, were bilateral both in their inner structure and their eccentric attachment to the substratum (Jägersten, 1955).

From the ancestral polyp another line was derived, characterized by the appearance of medusae and alternation of generations. The Scyphozoa preserve the original position of the germ cells and their liberation through the mouth. In primitive Scyphozoa, Lucernariida, and Cubomedusae, the polypoid and medusoid stages differ but little. Gastrulation by invagination occurs in many Discomedusae and the monodisc strobila may represent the first step of the transformation of a polyp into a medusa. Hydrozoan medusae still have gastric pockets and nearly always four radial canals (Hydroida); the polyps are simplified by decrease of size and formation of colonies. Aberrant types of gastrulation occur in blastulae that develop inside gonophores. Unipolar ingression as a vestige of invagination occurs in the more primitive blastular larvae. The highly specialized Siphonophora, the polypoid and medusoid persons of which arise nearly like organs in the very young larva, have been convincingly derived from gymnoblastic hydroids by Leloup (1929).

Jägersten (1955) supposes that the monaxial gastraea did not pass to the radiate polyp but to a creeping bilateral blastula and gastrula. The latter, the bilaterogastrula, was the ancestral form for the Porifera, Cnidaria, Ctenophora, and Coelomata (Bilateria), according to Jägersten. Since Haeckel, it is usual to associate bilateral symmetry with a mobile benthonic life. But I find it difficult to imagine that a ventrally ciliated animal, gliding over the bottom, then passes into a completely ciliated, free-swimming larval stage, and finally attaches itself to the bottom. Moreover, it is strange that the ancestral bilateral symmetry should have disappeared altogether in the Porifera, Hydrozoa, and Scyphozoa, and yet be retained in the Anthozoa; for the former groups are as sessile as the last. Not even in ctenophores is the supposed ancestral bilateral symmetry maintained, although pelagic life is not incompatible with bilateral structure, as the larvae and adults of marine Bilateria show. I think epigenetic processes are conditioned by internal factors. Outer conditions —creeping, swimming, attachment—are only additional (Goette, 1921), and eliminate or maintain the innovations. In the latter case, the animals are said to be adapted. In my opinion, bilateral symmetry in the Anthozoa is such a retained adaptive innovation; and I think the early phylogeny of the Metazoa can be understood without the premise of Jägersten's bilaterogastrula.

The Ctenophora have entodermal germ cells, an aboral sensory center, and a highly differentiated ectomesenchyme; they therefore cannot be derived from Hydrozoa. As the tetraradiate ancestral polyp with four gastric pockets probably had nematocysts, ctenophores with their adhesive cells can have arisen only before this ancestral cnidarian was differentiated. The nematocysts of the ctenophore *Euchlora rubra*, of which Jägersten questioned the origin, have been shown to be intrinsic (Picard, 1955). Cnidaria and Ctenophora have a short stem in common (Remane, 1954a; Jägersten, 1955), as is further indicated by the four gastric pouches and four comb-rows in the ontogeny of ctenophores. The same holds true for the location of the germ cells and the discharge of eggs and sperm (except in the Platyctenea). Parallelisms to anthozoan larvae in ctenophores are: locomotion by cilia, aboral concentration of the nerve plexus, and development of a pharynx and gastric septa during pelagic life. The pelagic ctenophores are the primitive members of the group, the creeping and sessile Platyctenea the modified ones. The latter pass through a cydippid larval stage and are only similar to, not closely related to, polyclads. The collenchyma of cteno-

phores is ectomesodermal, the parenchyma of polyclads entomesodermal; the ectomesoderm of the latter, the larval mesoblast that descends from the third quartet, only furnishes muscles and connective tissue of the pharynx. A reminiscence of the radial tetramery of ctenophores is revealed by traces of the cross in the embryo of the polyclad *Planocera*. This feature is, however, less distinct in polyclads than in mollusks and annelids. The transitory frontal organ of hatching polyclads (Kato, 1940) is comparable to the apical organ of anthozoan larvae, ctenophores, and trochophores. Gastrulation by epiboly, a modification of emboly occurs in ctenophores (combined with emboly) and in polyclads.

As first observed by Barrois (1877), cleavage stages of ctenophores are similar to those of ctenostomatous and cheilostomatous Bryozoa.

ORIGIN AND EVOLUTION OF THE BILATERIA

The frequently avowed relation between the planulae of Hydrozoa, which are stereogastrulae, and the Acoela is based merely on the small size, shape, and ciliated epidermis. Cleavage resulting in planulae is indeterminate, adequal, and radial, whereas it is determinate, unequal, and spiral in Acoela. The inner mass of the planula consists of entoderm, that of the Acoela of ectomesenchyme and material of the fourth duet and the macromeres, not definitely separable into enteroderm and endomesoderm. An entirely epidermal nervous system is exceptional in Acoela (Westblad, 1948); their brain and nerve strands have no parallels in hydrozoan planulae. If the latter became sexual, one would expect dioecious gonads located in epidermal folds, and not hermaphroditic mesenchymal germ centers as in Acoela. If the Acoela are considered to connect the Coelenterata with the Bilateria, as Graff proposed, the internal cavity of the Coelenterata lined with gastrodermis must have originated a second time in the Bilateria descendent from the Acoela. As the latter have copulatory organs, the process in many Bilateria of releasing sperm and eggs into the water must be secondary. This is difficult to imagine.

The Bilateria (Coelomata) may have evolved from anthozoan larvae or from ctenophores. Both groups are pelagic; with Heider (1914), I do not find it difficult to conceive the acquisition of a complete bilateral symmetry by a pelagic animal. Anthozoan larvae have an internal bilateral symmetry, and their gastric pouches are not so fundamentally four in number as are those of ctenophores. Evidently during evolution of the ancestral cnidarian polyp to that of the Anthozoa, a certain plasticity in the arrangement of the septa was acquired. The tetramerous scleroseptal arrangement of the Tetracorallia, for example, passes through a hexamerous stage (Hyman, 1940). The ctenophoran ancestry of the Bilateria is suggested by their well-developed sensorial plate that may be homologous with the apical organ of larvae and the brain of adults in later phyla. The nerve strands, intermediate between a diffuse plexus and true nerves (Heider, 1927); the development of muscles from mesenchyme cells; and the presence of incipient genital ducts support the assumption of the origin of the Coelomata from Ctenophora. The facultative invagination of the nervous strands in strongly stimulated ctenophores suggests how an insunk nervous system may have been acquired (Heider, 1927).

It is now evident that I accept the enterocoel theory originating with Sedgwick (1884), according to which the enterocoelous method of coelom origin is the original one and the enterocoel sacs are phylogenetically identical with the gastric pockets of Scyphozoa, Anthozoa, and Ctenophora. It follows that all Bilateria are coelomate or derived from coelomate ancestors—hence the terms Bilateria and Coelomata are here used as synonymous. I also regard this original enterocoel as combining the functions of a gonocoel and a nephrocoel.

The Bilateria then evolved from a common root along two diverging lines. Whether these lines are called Protostomia and Deuterostomia (Grobben, 1908), or Gastroneuralia and Notoneuralia (Ulrich, 1950), or Hyponeuria and Epineuria (Cuénot, 1952), or still other terms is not important. The main character designated by the terms Protostomia and Deuterostomia cannot be verified in every group of recent Bilateria, because these groups are fragmentary remains of an immeasurably long evolution that has led to an enormous heterogeneity in details. The divergence of the main lines is evidenced in the embryology of Spiralia, as contrasted with that of Echinodermata, as well as in the morphology of Arthropoda, as contrasted with that of Chordata. Comparative experimental embryology confirms the findings of comparative morphology, evidencing a protostomatous (spiralian) and a deuterostomatous

type of determination, both connected by common bilaterian characters (Schleip, 1929). The ancestral common root of the Bilateria can be constructed from the common characters of the protostomatous Tentaculata (Phoronida, Bryozoa, Brachiopoda) and the deuterostomatous Hemichordata (Enteropneusta, Pterobranchia). A close relationship between the Bryozoa Ectoprocta and the Pterobranchia cannot be doubted (Heider, 1914), and the homologies between Tentaculata and Hemichordata are not restricted to ectoprocts and pterobranchs (Heider, 1913, 1914; E. Marcus, 1934).

The body of members of the phyla Tentaculata and Hemichordata is tripartite, regionated into protosoma (absent in Gymnolaemata), mesosoma, and metasoma; the protosoma contains one coelomic sac, the mesosoma and metasoma a pair each. Fundamentally, the body consists of epithelial lamellae separated by structureless sustaining membranes. Enterocoelic formation of the body cavities occurs in ctenostomatous Bryozoa, Brachiopoda, and Enteropneusta. Cephalization occurs in Phoronida (Selys-Longchamps, 1907) and Enteropneusta. Coelomic pores occur in Ectoprocta and Hemichordata. The larvae in anascan cheilostomatous Bryozoa and Pterobranchia are of the same type (Braem, 1911; Correa, 1948), and buds are constituted of ectoderm and mesoderm in Bryozoa and Pterobranchia. Tentacular structures that occur in many tornariae furnish only supplementary characters for the connection of the phyla mentioned. Recent studies of the nervous system of Enteropneusta (Silén, 1950) and Phoronida (Silén, 1954) did not confirm previously supposed, more general similarities.

The group basic to the Protostomia and Deuterostomia contains embryologically defined Protostomia (Phoronida, Brachiopoda) and Deuterostomia (Enteropneusta), to which Ectoprocta and Pterobranchia can be added by comparison of the adult forms with Phoronida and Enteropneusta, respectively. Fundamental and other differences of the nervous and excretory systems explain why Boettger (1952) rejected Masterman's name, Archicoelomata, which Ulrich (1949, 1950) uses for these and related phyla (Pogonophora, Echinodermata, and perhaps Chaetognatha). Ulrich's idea is, however, quite sound; and his term can be used, not as a taxonomic division, but in the same sense as, for example, Spiralia.

The following reconstruction of the ancestor of the Bilateria (Coelomata) considers only Tentaculata (Phoronida, Bryozoa, Brachiopoda) and Hemichordata. One can suppose that this ancestor differs from anthozoan larvae and ctenophores by the presence of an anus; for in only one order of this first coelomate group, the higher brachiopods (Testicardines), is an anus wanting.

Was the anus of the first Bilateria a neo-formation as in the Protostomia, or did it correspond to the blastopore (prostoma) of the Deuterostomia? This alternative does not exhaust the possibilities of oral and anal differentiation. The blastopore can close and a new mouth and anus develop later, as, for example, in the Entoprocta; or the same development can take place because a blastopore never existed, as in tardigrades. Finally, a slitlike blastopore, or better oroproct, may divide into an anterior mouth and a posterior anus, as in *Polygordius* and the Onychophora. As mouth and anus frequently arise very near one another in a prostomial field, the latter type of origin of mouth and anus seems to be ancestral. Also the ectodermal pharynx of the presumed free-swimming precursor of the archioelomate groups divided, thus giving origin to stomodaeum and proctodaeum.

In an elongating animal that passes from the walnut shape of a ctenophore or an anthozoan larva to an elongated form, perhaps like a zoanthella larva, the cyclomeres become antimeres (Sedgwick, 1884). The protocoel is unpaired, mesocoels and metacoels paired. It cannot be decided whether one should suppose a coalescence of two anterior gastric pouches in the evolution from a hexamerous ancestor, or imagine an unpaired posterior primordium in a tetramerous animal that later divides. As sometimes two pores and an incomplete mesentery occur in the protocoel of Enteropneusta, and as two axocoels develop in the related Echinodermata, one would perhaps prefer the hexamerous origin. On the other hand, the axocoels (and other coelomic sacs) of echinoderms (except *Comatula*) begin with one unpaired sac at the apex of the archenteron, and a similar unpaired origin can easily be imagined for the metacoels. One may finally refer to the unpaired primordium (4d) of the metacoel in the Spiralia, the division of which is the first bilateral character in these radiate embryos. Although this last idea is supported only by animals not directly connected with coelenterates, I find it more important than the assumption of earlier or later bipartition of unpaired pouches. The details of the development

of the coelome are not uniform in either Enteropneusta or Echinodermata (Heider, 1910). With Remane (1954a) I assume a tetramerous ancestor, not a hexamerous one (Jägersten, 1955). The tetramerous beginning—one pouch in front, one behind, and one on each side—agrees well with Ulrich's synthesis (1950) of the oligomerous animal.

The walls of the coelomic sacs lodge the gonads, as in ancestors with entodermal origin of germ cells. In the Madreporaria, descendents of the Tetracorallia, excretory function of the epithelium of the gastric pockets is known (Hyman, 1940); the rosettes of the gastrovascular canals of ctenophores are also probably excretory (ibid.).

The origin of the excretory and circulatory systems, systems that must have been present in the ancestor of the Tentaculata and Hemichordata, can hardly be traced from the supposed tetramerous ancestor (anthozoan or ctenophoran larva). Both have, it is true, gastrovascular pores that might have been taken over as coelomic pores when the coelomic sacs constricted off. Whether a protonephridial system exists in platycteneid and atentaculate ctenophores (Krumbach, 1925) is problematical.

The archicoelomate phyla have excretory pores, protonephridia, and metanephridia. It is impossible to know which type of excretory system came first. In many cases larval protonephridia are substituted by metanephridia in the adult; but also the metanephridial funnel may close, in which case the excretory canal assumes a protonephridial character (*Chaetogaster diaphanus*). Open and closed micronephridia may occur simultaneously in the same earthworms (Stephenson, 1930). As the adult Phoronida and Brachiopoda are coelomate animals with metanephridia, as in many Protostomia and the craniate Deuterostomia, one can imagine that metanephridia were characteristic of the ancestral bilaterian, conveying both germ cells and excretory fluid.

The circulatory system, the lumen of which is blastocoelic, begins as an intestinal blood sinus between intestinal and splanchnopleuric mesoderm. Dorsal and ventral vessels develop between the bases of the cells that form the dorsal and ventral mesenteries.

The common ancestors (Protocoelomata of MacBride, 1914) of the Bilateria were probably predominantly epithelial animals with little connective tissue or parenchymal strands, possibly provided with a pair of tentacles on the mesosoma, and maybe with the anthozoan sulcus and sulculus that later appear as endostyle and epistyle.

RELATIONS WITHIN THE TENTACULATA

Among the Tentaculata, the Phoronida have the greatest number of archaic characters. The Brachiopoda are primitive, too, in the enterocoelic origin of their body cavities, which remain rather well separated in the adults. Metanephridia and a closed circulatory system occur in Phoronida and Brachiopoda, as do protosoma, mesosoma, and metasoma, which in ectoprocts occur only in Phylactolaemata. The latter are also primitive in the structure of the body wall, absence of polymorphism, shape of the zoid with lack of a protective apparatus at the entrance, and manner of development of polypide buds (Borg, 1926). The last two features are also found in the cyclostomatous ectoprocts. Indeed, Phylactolaemata and Cyclostomata resemble each other more closely than either resembles the Ctenostomata and Cheilostomata. The two latter are primitive in the budding of the cystids, development of the embryo, and structure of the cyphonautes larva. The close relationship between ctenostome and cheilostome ectoprocts, called Eurystomata by E. Marcus (1938) or Cheilo-Ctenostomata by Silén (1942), is puzzling in view of the great time interval between the early Ordovician, when the oldest known ctenostome appeared, and the middle Mesozoic, when the first cheilostomes became established (Bassler, 1953). The Cryptostomata with cheilostome features, existing from the Ordovician to the Permian, do not close the gap.

The Entoprocta can best be viewed as attached larvae of the Ectoprocta. They are trochophores with a very small hyposhpere, and the larvae of the archaic Bilateria may have been trochophorlike. The structure of the Rotatoria is also evidently similar to that of the trochophore. One can thus in some measure comprehend that Hyman (1951b) compares the Entoprocta, especially the loxosomatids, with the Collothecacea. The latter, however, are rather specialized rotifers (see Remane, 1933, p. 519). Cell constancy, syncytial tissues, unpaired germovitellarium and testis, cloaca, mastax, copulation as hypodermic impregnation by means of an eversible cirrus, minute males, absence of budding, and heterogony are characters which, in my opinion, exclude the Collothecacea from a relationship with the Entoprocta.

The spiral cleavage pattern of the Entoprocta is faintly indicated already in the Actiniaria (Pax, 1925), and hence in primitive Anthozoa, and also in Brachiopoda (Conklin, 1902) among the Tentaculata.

Unequal sets of blastomeres in the blastula approximate the cleavage pattern of cheilostomatous ectoprocts to the determinate type (Marcus, 1938), and Correa (1948) has compared their gastrula with that of the Spiralia. The scantiness of ectomesodermal elements, which is a deuterostome feature of Phoronida, Ectoprocta, and Brachiopoda, separates these groups from the Entoprocta. On the other hand the latter are, like phylactolaemates and enteropneusts, protaxial—an exception among the Bilateria. If the topography of the larval body is considered, the entoprocts direct their dorsal, active face towards the water, as in gymnolaemates. If the rotation that takes place during attachment is considered, the active face of entoprocts is ventral, as in phylactolaemates (Marcus, 1939, plate 30). The entoprocts attached with the hyposphere, as in gymnolaemates; but their ganglion is located as in phylactolaemates. Homologous organs in the larvae of entoprocts and ectoprocts are: apical plate, tripartite intestine, prototroch, and vestibular organ (adhesive sac). The preoral organ (Entoprocta) and the pyriform organ (Ectoprocta) are perhaps homologous, both being connected with the apical organ by a neuromuscular strand. The paired protonephridia of the Entoprocta have no parallels in the Ectoprocta. Budding, degeneration, and regeneration are very similar in the two groups; and location of buds on the oral side is the same in Entoprocta and Phylactolaemata.

If the assumption favored here, that of vertical relationship (Buddenbrock, 1932) between the Entoprocta and Ectoprocta, is rejected, one can only include the Entoprocta in the Platyhelminthes (Ulrich, 1950). In that case the similarity of entoproct and ectoproct larvae would be a surprising convergence. In the Platyhelminthes, the Entoprocta would have to form a distinct class that has sprung rather far from the Turbellaria and Nemertini. The inclusion of the Entoprocta in the Platyhelminthes would necessitate that, for this now well-delimited phylum, only a formula (Remane's diagrammatic type, 1952) could be set up.

The anterior archimetamere, the protocoel (axocoel), disappears already in the gymnolaemate ectoprocts, nor is it developed in the succeeding protostomatous phyla. Also the two middle archimetameres, the mesocoels (hydrocoels), are nearly always suppressed in the neocoelomate phyla (Remane, 1950). The blastomeres 4a, 4b, and 4c of the Spiralia—forms with spiral cleavage—correspond theoretically to the anterior and the middle archimetamers and become entomeres. The hinder archimetameres, the metacoels (somatocoels) of the coelomate phyla of the Spiralia, are produced by bilateral division of 4d. Influenced by segmental disposition of other organs (see Hyman, 1951a, p. 30, paragraphs 2 and 3), each metacoel is subdivided into generally 3 or 4 segments (Ivanow, 1928, 1933). These deutometameres are larval segments and become anterior trunk segments in the adults. The succeeding trunk segments in the Articulata, the tritometameres, develop in a posterior budding zone with participation of the ectoderm.

SPIRALIA, PLATYHELMINTHES, AND NEMERTEANS

Possibly the Sipunculoidea are the most primitive Spiralia. The cavities of their tentacles communicate with a circumoral coelom, perhaps a mesocoel. Their metacoel and ventral nerve cord are not segmented. Gerould (*in litteris*) has revoked his statement (1907) of a transitory segmentation of mesoderm and nerve cord in sipunculoids and declares a total lack of evidence of segmentation in his material; hence there remain no grounds for considering the sipunculoids as simplified annelids. Dawydoff (1928) also states that the coelom of sipunculoids is never metamerized. Metanephridia as gononephroducts already appear in the larva, as in brachiopods. Mesocoels are possibly also evidenced in the tentacular cavities, and ampullae in the archiannelid families Protodrilidae and Saccocirridae and in the median cavity of the prostomium of the sedentary polychaete *Psammodrilus balanoglossoides* (Swedmark, 1955a). However, these cavities may be also, in part, primary body cavity (remains of the blastocoel).

The Platyhelminthes belong to the Spiralia. Their primitive nervous system and the absence of budding tritometameres characterize them as an offshoot of the lower Spiralia. Most of their organs are simplified, not primitive, because an ancestral bilaterian must have had the fundamental features of the Archicoelomata, viz., three

coeloms, mouth, anus, vessels, and perhaps tentacles. Gastric pockets and coeloms filled with liquid sustain the body; such a hydroskeleton serves as support for the action of dermal muscles. In case of locomation by cilia, as in small Turbellaria, or by a ventral foot (Mollusca), a coelom is unnecessary. It can also be substituted functionally by intestinal diverticula (dendrocoelate Turbellaria), by dense parenchyma (flukes, tapeworms, nemerteans), by a spacious pseudocoel (Aschelminthes), by adhesive disks (Hirudinea), or by an exoskeleton (Arthropoda). The leeches prove that a platyhelminth-like organization can arise from coelomate worms (Oligochaeta). The reduction of the coelom in Platyhelminthes has necessarily involved loss of the circulatory system and of the mesodermal funnels of the excretory ducts. In compensation, proper gonoducts have arisen in incredible diversity. Small Turbellaria with correspondingly large surface that live in an isotonic medium, the Acoela, lack excretory organs. Loss of the anus, also in non-parasitic Bilateria, is frequent (Marcus, 1934; further examples in Remane, 1951). Remane sets forth an attractive theory that in platyhelminths the ancestral intestine communicated by a bursa with a cloaca that also received the oviducts (his fig. 2). Syncytial tissues and absence of an intestinal cavity make it difficult to consider the Acoela as the most primitive Turbellaria (Böhmig, 1895; Karling, 1940). Ancestral turbellarian characters are scattered among several orders, as Macrostomida and Polycladida, the latter with larvae representing simplified trochophores; but brain, pharynx, and intestine of polyclads are complicated. Catenulida also show primitive characteristics.

Some characters of the original turbellarian (Remane, 1952) can be assumed, although details of the homologies have not yet been established. There was an epithelial ciliated epidermis with a complex of frontal glands; a subepidermal nerve plexus; and anterior brainlike nervous concentration, perhaps containing a statocyst and connected with 3 or 4 pairs of longitudinal nerves; and an epithelial, ciliated intestine with a pharynx simplex and a hind gut (bursa of the reproductive system). The last opened into a cloaca as in Remane's diagram (see above). The eggs were entolecithal; and the spiral cleavage was like that of polyclads, not like that of acoels.

The evolution of the Trematoda from the Dalyellioida, as postulated by Meixner (1926), was accepted by Fuhrmann (1928–1930). For the Monogenea, an origin from the dalyellioid Temnocephalida is worthy of consideration. Also the Cestoda, in the past derived from the Trematoda or Cestodaria, are now considered as stemming from another dalyellioid family, the Anoplodiidae (Meixner, 1926) to which the Tetraphyllidea, as the most primitive cestodes, are connected (Fuhrmann, 1930–1931). The origin of the Amphilinidea and Gyrocotylidea is not known, but Fuhrmann and others regard the former as neotenic tapeworms.

I regard the nemerteans as an independent branch of the lower Spiralia, the root of which may have lain not far from that of the Turbellaria. All authors consider the Palaeonemertini as the most primitive order. Their nervous system is epidermal; from this original position it gradually sinks into the mesenchyme in the more specialized orders (Hyman, 1951a). "The slow and orderly way" of the development of the paleonemertean *Cephalothrix* (Smith, 1935) shows reminiscences of polyclads. Among the nemertean larvae, the pilidium, more primitive than Desor's larva, is similar to Goette's polyclad larva. Absence of anus and nephridium in both cannot be explained merely as an adaptation to pelagic life. Goette's larva and the pilidium are more than similar "Lebensformtypen" (Remane, 1952).

In the primitive direct development of *Cephalothrix* the hind gut appears late—evidently not as a proctodaeum, but as an entodermal production. Also the bursa, which I suppose to be the original hind gut of the Turbellaria, is not proctodaeal. Where a proctodaeal invagination occurs in nemerteans, this is short and perhaps homologous with the theoretically assumed turbellarian cloaca. For instance, the genital antrum of triclads, which orginates in connection with the bursa, may correspond with this cloaca.

According to Smith (1935) heteronemertine development with a larva is closer to direct anoplous development than to that of the Enopla. In the latter, e.g., *Malacobdella* and possibly also *Cephalothrix*, the four so-called teloblasts are ectomesodermal. They are consistent with the larval mesoblast of polyclads in number and in origin from the second quartet.

The descriptions of the development of an entomesoderm from 4d or more micromeres of the fourth quartet in nemerteans (Nusbaum and Oxner, 1913) are in many cases rather vague, and segmentation of the entomesodermal bands is never indicated. The so-called metameric features of the nemertean body correspond to the pseudometamerism of the turbellarian groups Proseriata and Tricladida. The Hirudinea, with

a rigorously segmented primordium of the coelom, are not related to nemerteans, except that both are Spiralia.

As nemerteans and turbellarians in my opinion have arisen from coelomate Bilateria, coelomic vestiges might be sought in both; for instance, the partially ciliate female ducts of polyclads are perhaps coelomic remants. Such remainders appear more clearly in nemerteans, i. e., coeloms are presumed in the rhynchocoel and the lateral vessels. Furthermore, in the arrangement of the genital sacs and the possession of an anus, nemertines appear more primitive than turbellarians. The layer of cells that lines the rhynchocoel comes entirely from a somatopleure (Nusbaum and Oxner, 1913). The lateral vessels arise as outgrowths of the head cavity, Bürger's archihaemal space, that is lined with somatopleuric and splanchnopleuric mesoderm. These layers, it is true, arise by epithelial disposition of mesenchyme cells of which the origin as ectomesodermal or entomesodermal is indecisive.

The lateral vessels of the Palaeonemertea are closely connected with the excretory organs, the terminal chamber of which (Coe, 1930) protrudes into the vascular lumen. Whether these nephridia are metanephridia (Coe, 1930; Navitzki, 1931; Friedrich, 1935) or protonephridia (Hyman, 1951a) is debatable, as they are not typical of either kind. The character of the nephridia in either sense does not prevent considering the lateral vessels as coelomic remants. These vessels present a case of parallel evolution with the secondary circulatory system of leeches (Arhynchobdellida). Also the similar proboscis of kalyptorhynchid rhabdocoels and of nemerteans must be considered analogous, not homologous, as these most highly specialized Turbellaria are not directly related to nemerteans. The primary foregut of nemerteans and the embryonic pharynx of triclads are further similar organs without evolutionary significance. For the general similarities between nemerteans and flatworms, I refer to Hyman's phylogenetic considerations (1951a). The head glands, which she justly mentioned, develop very early in the primitive ontogeny of *Cephalothrix*.

RELATIONSHIPS AMONG THE ASCHELMINTHES

Most of the Aschelminthes are simple animals without organs beyond those generally present in Bilateria. Some authors, therefore, reject the evolutionary relations of the classes united under the Aschelminthes and consider them isolated groups of worms. Others try to unite too many classes in the phylum, principally by negative characters. The nematodes attain an evolutionary culmination among worms; with uniform organization and possibly half a million species (Hyman, 1951b), they have conquered all biotypes. Why then does Naef (1931) speak of the "inglorious way of the evolution of this accumulation of rubbish"?

Among the various theories that try to establish the ancestry of the Rotatoria, that which considers them as related to trochophorelike forms, simple or simplified annelids (Remane, 1929–1933), has some plausibility. The famous globular *Trochosphaera* that belongs to the specialized Floscullariacea has lost its phylogenetic significance, since similar sacciform or nearly spherical pelagic forms were discovered in several families (Beauchamp, 1909). All authors agree in regarding the Seisonidea as the most primitive Rotatoria. Though the corona of these ectoparasites is reduced, their remaining anatomy and reproductive biology are ancestral.

The concept that the Rotatoria are more closely related to the Annelida than to the Turbellaria is supported by the morphology and histology of the stomodaeum, especially that of the pharyngeal musculature (Jägersten, 1947). These studies have also shown that, apart from the Polygordiidae, the remaining families of the Archiannelida are relatively closely allied. One need by no means regard the Dinophilidae as intermediate forms between Annelida and Rotatoria. The similarities of the dinophilids with annelidan metatrochophores can well be indicative of reduction by which larval features frequently become definitive. Whether neotenic annelidan larvae or annelids that have become larva-like by reduction have given rise to the Rotatoria remains undecided. Not to establish homologies but to stress similarities, I mention that the haptic lobes of *Diurodrilus* are comparable to the toes of the Rotatoria. Three species of *Diurodrilus* have four toes, as in many bdelloids (for bibliography see Gerlach, 1952, 1953). It is true that an ancestral type of the Rotatoria without toes must be presumed (Remane, 1929–1933). The large cephalic ring of cilia in *Dinophilus* can be compared with th circumapical field, the antero-ventral ciliation of *Diurodrilus* with the buccal field of rotifers. Sensory hairs of *Diurodrilus*

and *Dinophilus* are similar to the dorsal and lateral palps of rotifers. With the exception of the Gastrotricha, *Diurodrilus* contains the animals most similar to rotifers. According to Hanström (1926), the nervous system of rotifers is more similar to that of annelids than to that of turbellarians.

The orange-colored species of *Dinophilus* have males and females of equal size, and their eggs are monomorphic as in the Seisonidea. The white species, possibly only one, *D. gyrociliatus*, has dimorphic eggs and dwarf males (bibliography in Eveline Marcus, 1948) as in the Monogononta. This last likeness is merely to be evaluated as convergence or perhaps parallel evolution from similar ancestors. In a marine organism like *Dinophilus*, the occurrence of obligatory encystment is remarkable; encysted worms survive inclusion in ice (Jägersten, 1951).

The ontogeny does not permit further comparisons although dinophilids have direct development like rotifers with a modified spiral type of cleavage. But in *Dinophilus* the coelom is represented by the ample cavity of the gonad and by lateral and ventral spaces (Jägersten, 1944). Further, the nephridia of *Dinophilus*, connected with the coelom, probably have an entomesodermal (coelomomesodermal) terminal chamber and an ectodermal or ectomesodermal middle and distal part (ibid). Nephridia and nervous system are distinctly metameric.

The cleavage of rotifers recalls the spiral type in the arrangement of the first blastomeres and the formation of four quartets. A large blastomere from the D-quadrant passes into the interior and originates the gonad. The enclosing syncytium of the gonad does not originate from this blastomere but from cells detached from the blastoderm. At present, while only the embryology of the highly specialized *Asplanchna* is known, no trace of a coelom is to be found in rotifers. Their nephridia are typical protonephridia, with flame bulbs. Their pseudosegmentation diminishes from the primitive Seisonidea, in which it is very pronounced, to the more specialized Monogononta.

Organs which functionally belong to the reproductive apparatus, viz., the male bursa and female uterus and vagina of the Acanthocephala, are morphologically parts of the original intestine. The derivation of the Acanthocephala from the Rotifera has been advocated by von Haffner (1950).

The Gastrotricha occupy an intermediate position between the Rotatoria and Nematoda in many characters (Remane, 1935–1936). The Rotatoria, with mastax, gastric glands, and high differentiation of the various parts of the digestive tract, are more specialized than the Gastrotricha and are more primitive only in the frequent ciliation of the intestine. Therefore one cannot derive the Gastrotricha from the Rotatoria, but can only suppose a common origin for both. In both groups a descent from a trochophore-like simple or simplified annelid leaves less gaps to be filled out with hypotheses than a descent from the Turbellaria. The two orders of Gastrotricha are united anatomically and embryologically (Swedmark, 1955b).

As the nematodes are closer to gastrotrichs than to rotifers, they must have arisen from the evolutionary line that ends with gastrotrichs long after the bifurcation into rotatorian and gastrotrichan lines had taken place.

The Nematomorpha are allied to the Nematoda, especially by the nectonematoids that have both dorsal and ventral epidermal chords. This order will perhaps in the future be included in the Nematoda (Hyman, 1951b). But also for the Gordioidea, Heider (1920) has shown numerous similarities with nematodes, especially with trichuroids. Also the Mermithoidea, a much more primitive order of nematodes, may in anatomical and biological respects be considered a possibility for the origin of the Nematomorpha.

The general organization of the Kinorhyncha fits into the Aschelminthes. The kinorhynchs have several characters in common with gastrotrichs and especially nematodes, less with rotifers. They are separated from the central aschelminth group (rotifers, gastrotrichs, nematodes) by their possession of a two-layered pharynx, a "highly disagreeable fact" (Remane, 1935–1936). The syncytial pharyngeal epithelium that produces the cuticular lining is separated from an outer layer of radiate muscles by a distinct membrane. Outside the latter, annular fibers seem to occur in *Cateria styx* (Gerlach, 1956). Until the development of the pharynx is known, it is impossible to derive the kinorhynchs from any of the central groups of aschelminths, the pharynx of which is constituted of one epithelial layer in which the muscle fibrils originate.

The segmented integument, the segmented ganglionated ventral nerve cord, the segmentally arranged muscles, and the serial posterior development of zonites (Nyholm, 1947, text fig. 12) support the opinion of an annelid descent of kinorhynchs, with reduction of coelom and circulatory

system, but preservation of segmentation. As, however, intermediate forms between annelids and kinorhynchs and the development of the latter are unknown, the origin of kinorhynchs remains uncertain.

We are ignorant of the origin of the priapulids; and even the position of these three species of protostomatous, wormlike animals is uncertain. Whether one includes them in the Aschelminthes (Hyman, 1951b) or in the Annelida (Boettger, 1952) depends on one's opinion of the structureless membrane without nuclei that lines the body cavity. As Hyman (1951b) has said, "the presence of complete circular and longitudinal muscle layers in both body and intestinal walls" is suggestive of coelomate animals, but such layers also occur in the turbellarian *Stenostomum*, the spacious and rather empty body cavity of which classifies as a blastocoel. On the other hand, the priapulid pharynx differs completely from that of the central aschelminth groups; it is comparable with that of the kinorhynchs; and also some other features are similar in both. Whether these similarities are homologies is uncertain, and moreover of little value, as the position of the kinorhynchs is also doubtful.

My small material of *Buddenbrockia plumatellae*, parasitic in the coelom of fresh-water ectoprocts (Marcus, 1941), and supposed to be a reduced nematode, showed no sperms; and therefore the possibility that it is a trematode sporocyst could not be excluded.

Adults and larvae of the Phoronida, and the cleavage, coelom development, and larval type of the Brachiopoda, contain the elements with which the line of the Spiralia began. The main direction of this line runs to the Mollusca and Articulata, perhaps by way of the Sipunculoidea; the Platyhelminthes and probably also the Aschelminthes are side branches.

MOLLUSCA

Head, visceral sac, mantle, foot, and shell characterize the Mollusca. The shell developed within the phylum from a dorsal cuticle that covered the thin-walled visceral sac. The foot is a ventral thickening of the skin musculature. The head comprises the regions of the apical plate and the mouth.

The ontogeny and anatomy of the nervous system of the lower Mollusca agree with those of the Turbellaria (Hänstrom, 1928); in primitive annelids the turbellarian plan of nervous system is even more reduced than in lower mollusks. In comparing the nervous system of the Turbellaria and Mollusca, one must consider the Solenogastres rather than the Placophora, inasmuch as the latter have secondarily reduced head and cerebral ganglia (Hoffmann, 1937). Reduction may also explain the absence in Placophora of ganglionic thickenings present in the longitudinal connectives of Solenogastres. The similarity of the molluscan buccal loop and the stomatogastric nervous system of some polychaetes (Pelseneer, 1899) may be viewed as a product of parallel development, because an orthogonal nervous system must be assumed for the common ancestor of the Spiralia.

The Mollusca cannot, however, have originated from the Platyhelminthes. *Rhodope veranyi* once considered a link between these phyla, is not primitive, but a very much reduced nudibranch (the Marcuses, 1952) that perhaps belongs to the Doridacea (Boettger, 1954).

Cuticle, circulatory system, and metanephridia separate the Mollusca from the Turbellaria. A richly developed mesenchyme occurs also in leeches. Ventral cilia in the archiannelids Nerillidae and *Protodrilus*, and dorsal ones in these and especially in *Dinophilus* and some polychaetes show that a ciliated epidermis (Söderström, 1920) is not necessarily a turbellarian character. The complex of organs that comprises pericardium, heart, gonad, and kidney in molluscs does not exist in the Turbellaria. As this complex develops tardily, when the mesodermal bands have already dissolved, its coelomic nature (Dawydoff, 1928 Korschelt, 1936) is contested by competent malacologists (Hoffmann, 1937). The cleavage (Conklin, 1897, and others) and the larvae, especially the preveliger stages of mollusks, agree with those of annelids. Hence one can accept the mollusks as coelomate Spiralia. Their coelom, constituted of the originally paired pericardium and the cavity of the gonad, is homologous with the larval coelom of annelids; both are deutometameres, i.e., coelomic parts originated by partition of a metacoel. According to this interpretation, a common origin of the Mollusca and Annelida can be presumed. The mentioned molluscan characters are all compatible with this idea. Pelseneer (1899) further compared the radular pouch that appears early in the larvae of primitive prosobranchs with the ventral pharyngeal sac of archiannelids and several polychete families (Schlieper, 1927). Heider's study of the

Eunicidae (1925) shows plates remotely similar to a radula, and the formation of the teeth (Heider, 1923) has a general likeness to the development of radular plates.

Mention should be made of the newly discovered archaic gastropod, *Neopilina galatheae* (Lemche, 1957), a living tryblidacean, a primitively orthoneurous mollusk with a thin shell in a single piece, five body metameres, and five pairs of nephridia, which convey the genital products. It forms a link between the Polyplacophora and the nautiloid Cephalopoda; its radula is located as in the Solenogastres; and the branchial ganglion for each gill, as well as the dextrally coiled larval shell, are gastropodan features. A segment of the gill-bearing region of *Neopilina* is closely similar to a typical annelid segment.

The Solenogastres are primitive, vermiform Mollusca (Paramollusca) (Hoffmann, 1937); they lack a mantle. Whereas in mollusks without a shell this generally appears in the ontogeny, the Solenogastres have none at any stage (Baba, 1938, 1940). Only transitory scalelike plates have been described in the larvae of two species (Pruvot, 1890, 1892). As the most specialized Chaetodermatidae lack a ventral furrow, this ciliated organ with its pedal gland in the other families is evidently a reduced foot (Boettger, 1955). In the young trochophore of *Epimenia*, the ciliated ventral furrow is broader than some hours later. The prelarval stages of the Solenogastres are similar to those of the Polyplacophora. In one species (Pruvot, 1892) the hind part of the adult body emerges from a posterior cavity of the larva, and thus recalls the development of the metasoma in phoronids.

As the Polyplacophora (Loricata) agree with Solenogastres in their nervous system and paired gonads, these two groups must descend from a common root. Their back, with eight shell plates and separated from the foot by an annular fold, approximates that of the higher Mollusca (Conchifera), but the latter must have evolved already in precambrian times (Naef, 1931), since the oldest bilaterally symmetrical snails (Amphigastropoda) and the streptoneurous prosobranchs (Diotocardia) are present already in the Cambrian. As the shell of the Conchifera develops as a uniform membrane and the nervous system differs widely from that of the Loricata, the latter cannot be their direct ancestors. For a phylogeny of the prosobranchs, I refer to Thiele (1935).

The Heteropoda are pelagic Mesogastropoda (Taenioglossa), evolved from the strombacea.

The evolution of the Euthyneura, viz., Opisthobranchia and Pulmonata, has been recently studied by Boettger (1954). His system considers all modern results. The group Pteropoda is disssolved, and the mostly shelled Thecosomata form two branches of a stem coming from the Acteonidae; the shell-less Gymnosomata have a common root with the Anaspidea (Aplysiacea) in the Aceridae; the Pyramidellidae derive from the Acteonidae (Fretter and Graham, 1949); and the Onchidacea are removed from the Stylommatophora (Fretter, 1943). The streptoneurous opisthobranchiate Acteonidae gave origin to the other Cephalaspidea (Tectibranchia) and to the Basommatophora, near the root of which the Siphonariidae stand. By way of families of coastal life, one evolutionary line continued to the most primitive fresh-water Basommatophora, the Chilinidae with a twisted visceral loop, standing at the root of the Limnaeidae and Physidae-Planorbidae. Another line went to the coastal Ellobiidae, the root of the Stylommatophora. For the origin of the other euthyneurous orders from the Cephalaspidae, I refer to Boettger (1954).

As the Acteonidae, unanimously accepted as the ancestral group of the Euthyneura (Fretter and Graham, 1954), begin in the Paleozoic (Mississippian), and as also the first Stylommatophora are only slightly younger (Pennsylvanian), not the Monotocardia but the Diotocardia, perhaps the Loxonematidae or Subulitidae, must be viewed as ancestral to the Euthyneura.

The asymmetry of the Prosobranchia might have begun with the reduction of the left gonad (Thiele, 1935). The gonads are in fact paired in the less specialized Solenogastres and Loricata, whereas the Gastropoda have but a single gonad. The reason for this reduction is unknown and cannot be presumed to be a phylogenetically secondary one-sided copulation. The weight of the visceral mass is supposed to have caused the shell to incline to the left, until it touched the bottom and hindered locomotion. Hence the shell aperture and with it the pallial organs were gradually removed along the right side toward the anterior end. The "tendency to detorsion" in the Euthyneura has no explanation.

The Scaphopoda are a side branch of the line that proceeds to the Bivalvia. Like the bivalves, scaphopods have an elongated, but not high (as in the Gastropoda or Cephalopoda), shell that develops from a bipartite stage by concrescence of the ventral mantle borders. Their nervous system is similar to that of the Nuculidae, some of which have the same primitive pleural ganglia at the root of the visceral commissure. But relations exist also to primitive Gastropoda (presence

of buccal ganglia) and even to the Loricata (presence of a subradular organ). Lamellibranch features of scaphopods are the protractile digging foot and broad mantle. The head is less reduced and the circulatory system more reduced (with retention of the ventricle only) than in bivalves. Gills are absent. The unpaired gonad in the rear part of the body unites when mature with the right kidney that opens into the mantle chamber; this is a primitive gastropodan character (most of the Diotocardia).

The slit and slit band of the Pleurotomariacea suggest how the bivalve shell was derived from an ancestral univalve shell, probably a low cap, by a median partition. The periostracum remains continuous, forming the ligament. As in scaphopods, the shell is elongated. The most primitive bivalves are the Protobranchia, with flat gill filaments disposed in two opposite rows on the branchial axis. Distinct pleural ganglia, plantar ventral surface, simple kidneys, openings of the gonad into the renopericardial duct, and other characters are primitive. Appendages of the oral lobes can be protracted for feeding, in the primitive Nuculacea. The hinge teeth are numerous and uniform (taxodont: Nuculacea), or poorly defined and even absent (Solenomya). The filibranch orders, of which I mention only the taxodont Arcacea, evolved from the protobranchs by the bending upward of the terminal portions of their gill filaments. Protobranchs and filibranchs appear in the Ordovician, hence their differentiation must have occurred at the beginning of the Cambrian or earlier. Bivalves change with unusual slowness. Their main lines begin early and are very persistent, having diverged into two lines already in the Paleozoic. One, the filibranch Anisomyaria, with gradual reduction of the anterior adductor, begins with the primitive Mytilacea and Pteriacea (Aviculacea) in the Ordovician and leads to the Pectinacea and Ostreacea. The other line is that of the eulamellibranchiates, in which the reflexed gill lamellae are as a rule laterally joined by interlamellar junctions that form enclosed spaces. The earliest suborder (Trigoniacea) appears in the Ordovician; the Unionacea are younger (Triassic). The largest suborder, the Heterodonta, begins in the Silurian and is the most prominent in modern marine faunas. The hinge has cardinal and frequently lateral teeth on the anterior and posterior portions of the hinge plate. From the heterodont Tellinacea the suborder Adapedonta was derived (viz., *Solen*, *Mya*, *Teredo*), and from these the hermaphroditic Anomalodesmata, to which belong among others the Poromyacea, with horizontal reduced gills, mostly in deep water.

The shell of the Cephalopoda is raised conically, as in snails, but has preserved bilateral symmetry. This group passes from the assumed creeping mode of life of the archaic Conchiferes to a predatory pelagic life. They produced gas that accumulated in a buoyant chamber located in the shell apex. The enlarging body brought forth successive gas chambers separated by calcareous septa and remained connected with the shell apex by a strand passing through septal pores or a tube (siphuncle). The grasping tentacles formed by the foot and supplied by the pedal ganglion migrated toward the head between eyes and mouth. The bilateral symmetry, the posterior position of the pallial cavity, the communication between pericardium and gonocoelom (as in Solenogastres), and the separate gonoducts and nephridia are primitive features of cephalopods. They suggest that cephalopods have evolved before gastropods, scaphopods, and bivalves had separated.

The ancestral, pelagic forms of the Cambrian (the Nautiloidea) were straight or curved. Already in the Ordovician, coiled lines arose among them. *Nautilus* is primitive in its three broad, transversely disposed ganglionic cords that correspond to the cerebral (dorsal), pedal (anteroventral), and pleurovisceral (posteroventral) cords of the Solenogastres and Loricata. Early Devonian nautiloids, probably straight forms (*Bactrites*), gave origin to the Ammonoidea, which have a marginal siphuncle and fluted septa that make a strong but light shell possible (Moore, Lalicker, and Fischer, 1952). The ammonoids reached peak development during the Mesozoic, but vanished before the beginning of Cenozoic time, after having attained a diameter of 2 m. in the Cretaceous. Many were energetic swimmers; some, with irregular shells, as *Nipponites*, were bottom-dwellers, probably in a fixed position.

Nautiloids are Tetrabranchiata, and so possibly were the Ammonoidea. The first Dibranchiata are the first straight, and later curved, Belemnoidea, evolved in the Mississippian from straight-shelled Nautiloidea, possibly related to *Bactrites*. They resembled modern squids both in appearance and in mode of life. They reached a climax in Jurassic and Cretaceous times and were last represented in the Eocene. Sepioidea and Teuthoidea first appear in the Jurassic, probably as offshoots of the Belemnoidea. The Dibranchiata no longer have nerve cords. In the Decapoda (Decabrachia of Boettger, 1952), rather long connectives are still present. In the Octopoda, discovered to occur in the upper Cretaceous but certainly much older (Naef, 1931), all central ganglia are intimately united. Ancestral Prototeuthoidea, from which the Dibranchiata must have originated, were postulated by Naef (1923). His prediction was confirmed in many details by Pick-

ford's studies (1940, 1950, and others) of *Vampyroteuthis*, representing an ancient dibranchiate order, the Vampyromorpha. Primitive, for example, is the spacious, unconstricted coelom that surrounds heart, gonad, and branchial heart appendages, and communicates by a slender canal with an apical coelomic sac. Wide coelomoducts open into the kidney sacs, and the oviducts leave the anterior part of the coelom close beside the coelomoducts to open at the gill bases. The well-developed gladius resembles that of mesozoic forms; the fins rest directly on the shell sac; the caecum is rather simple; there are no anal valves, ink sac, or muscle provision for the chromatophores. The large spermatophoric glands project freely into the coelom. Decapodan traces (gills, brain, forwardly projecting dorsal mantle margin in youngest larvae), a few octopodan features (pancreas completely incorporated into the compact liver), and transitional characters (veins intermediate between the decapodan closed system and the octopodan system with many sinuses) complete the organization of this "living fossil." Transversely striated muscle fibers (mangle, funnel, retractor, fin) and double metamorphosis are specialized characters.

Phylogenetically unrelatable is the shell of the female *Argonauta* that so strikingly resembles the shell of some Cretaceous ammonoids. Naef (1923) presumed that the ancestral *Argonauta* appropriated empty ammonite shells, as at present the males of the related *Ocythoe* occupy empty *Salpa* tunics; then the dorsal arms gradually became adapted to the form of the ammonite shells and used their own glands for further construction and for dissolution of the alien septa. To confirm this idea ammonite shells to which new material is patched must be found.

ARTICULATA—ANNELIDA

With segments developing in a budding zone (tritometameres), a ladder-type ventral nervous system, and jointed locomotor appendages, the Superphylum Articulata terminates the main line of the Spiralia; and with chitinous cuticle, jointed legs, wings, tracheal respiratory system, and subdivision of the life cycle into successive, specialized stages (the holometabolous Pterygota) the pinnacle of metazoan organization is achieved.

The cephalic lobe (prostomium) of an annelid corresponds to the prosoma or apical region of the trochophore; it develops the brain, or part of it, and lacks coelom. The buccal segment (mesosoma) also lacks coelom, except perhaps in some archiannelids. The 3 or 4 anterior segments of the metamerized trunk (metasoma) are larval deutomeres, the hinder segments tritometameres developed in a preanal budding zone. This last is followed by a pygidial lobe representing the nonsegmented perianal region of the larva.

Worms simpler than this plan, especially as regards the body cavity, may be more primitive or secondarily reduced. The embryology and morphology of related forms must decide between these two possibilities. The problematical Ctenodrilidae, for example, were recognized as close to the Cirratulidae; the Histriobdellidae, nearly without dissepiments and without a blood-vascular system, are reduced Nereimorpha, close to the Eunicidae. Most Archiannelida are reduced polychaetes of various families. Because of retrograde phyletic processes, larval characters frequently become definitive, hence some archiannelids (Polygordiidae, Dinophilidae) show features that must be supposed for polychaete ancestors. In recent polychaetes the prostomium is modified by cephalization of peristomial and metastomial elements, or is restricted and substituted by the buccal segment (Siewing, 1953).

The parapodia may have evolved from organs similar to the paired adhesive glands of some *Protodrilus* species (Jägersten, 1952); these glands are segmental lateroventral projections. Jägersten surmises that their secretion became the setae, projecting from the opening and depressed into the setigerous sacs; by differentiation of the muscles of the latter the setae became mobile. According to this idea, the parapodia originally combined adhesive and lever functions.

The Polychaeta are the primary class of the Annelida. The free-living, predatory, so-called Errantia with rather uniformly constructed segments are more primitive than the so-called Sedentaria, which possess differentiated body regions. The ciliated tentacular crown of some ciliary-feeding tubicolous polychaetes develops from the ciliated peristomial region of the trochophore and therefore is possibly homologous with the lophophore (mesosoma) of the Tentaculata. Errantia and Sedentaria are known since the the Cambrian; the parasitic Myzostomida, a derivative of the Errantia, since the Carboniferous.

The gap between the Polychaeta and Clitellata cannot as yet be bridged. One can indicate neither the polychaete group from which the oligochaetes sprang nor the ancestral family of the latter. The greatest number of primitive characters is united in the oligochaete family Aeolosomatidae,

viz., ciliated locomotive prostomium, ciliated cephalic pits, a nervous system continuous with the epidermis, separate cords of the ventral nerve cord, union of the dorsal vessel and intestinal blood sinus in the middle and hind parts of the body, a ciliated gut, presence of nephridia in nearly all segments with occasionally a nephridium beginning in the peristomial segment, no true male ducts but this function served by unaltered nephridia, and non-localized production of germ cells (E. Marcus, 1944). The diffuse and imperfect clitellum is not necessarily primitive inasmuch as other characters of the reproductive system are certainly reduced (Eveline Marcus, 1944). The coelom has also retrogressed, a process that attains its maximum in *Rheomorpha* (Ruttner-Kolisko, 1955). Hence it appears impossible to derive other oligochaete families from the Aeolosomatidae, as Michaelsen (1928) did; the latter are not reduced Naididae (Stephenson, 1930), but a primitive side-branch of the Oligochaeta (Sperber, 1948).

The Lumbriculidae, Stephenson's root of the Oligochaeta, have a lumbricidan arrangement of the setae and gave origin to the terrestrial families. However, they cannot be the ancestors of the families Naididae and Tubificidae, to which the Opistocystidae are related. The hair bristles of this group of three oligochaete families indicate polychaete-like forerunners. The embryology of the Tubificidae is more ancestral than that of the Naididae, as the development of the latter differs from that of polychaetes and tubificids by the presence of a periblast around the embryo. Perhaps the Lumbriculidae derive from the Tubificidae; otherwise one must admit two divergent lines of ancestral oligochaetes, the tubificid–naid, and the lumbriculid–phreoryctid, with the Aeolosomatidae as a blind side-branch near the root. Yamaguchi (1953) gives a similar phylogenetic tree.

The evolutionary line from the Oligochaeta to the Hirudinea begins, according to Livanow (1931), with the Phreoryctidae (Haplotaxidae), (which are closely related to the Lumbriculidae. Within the Oligochaeta a side-branch of this line goes to the Branchiobdellidae, devoid of setae and with jaws and a posterior sucker but resembling the Oligochaeta in coelom, muscles, and position of the testes anterior to the ovaries (Michaelsen, 1919). The parenchymatous *Acanthobdella*, through "chaetopod," is a primitive leech, but not ancestral to other suborders of leeches (Autrum, 1939). The latter constitute two divergent lines, the more primitive Rhynchobdellae and the more specialized Arhynchobdellae (Gnathobdellae and Pharyngobdellae). To the Hirudinea possibly belongs a fossil from the upper Ordovician (Utica shale).

Of the group Gephyrea, the Echiuroidea are are least distant from annelids. Well-known echiuroids have a long, ventrally ciliated prostomium, a larval character, also found in *Diurodrilus*, *Nerilla*, and aeolosomatids, and further taking a proboscidiform shape in many naidids and in *Opistocysta*. The echiuroid coelom is undivided, as in many reduced polychaetes and in aeolosomatids; the gonoducts are modified metanephridia. Usually one to four pairs of the latter are present; the multiplication suggests reduced metamerism. The paired anal vesicles begin with one funnel each, and hence correspond to posterior metanephridia. The chitinoid setae are imbedded in follicles and are produced and replaced in a chaetopod manner. The diagonal muscle layer of the body wall lies internal to the circular and longitudinal layers, whereas it lies between the circular and longitudinal layers in leeches, branchiobdellids, and some limicolous oligochaetes (Stephenson, 1930); nevertheless this difference cannot be used to distinguish echiuroids from annelids (Newby, 1940), nor can the ectodermal contribution to the body musculature, as the circular muscles of annelids are ectomesodermal. The closed vascular system, with its ventral and dorsal vessels and intestinal sinus, is annelidan. A collateral intestine occurs also in the Capitellidae and a long and differentiated gut in *Stylarioides*. The ventral nerve cord develops by coalescence of two primoridia, as in annelids, and is transitorily segmented into ganglia. Cleavage shows an "annelidan cross." Teloblasts and transitory metamerism of the mesodermic bands are denied to exist, except for an observation of Dawydoff (1930). As non-annelidan features, Newby (1940; Pickford, 1947b) stressed the development of the mouth and the absence of a proctodaeum, which are also, however, true of *Tubifex* and *Glossiphonia*. The formation of mouth and anus by division of the blastopore is not "typically annelidan," as it does not occur in the Clitellata, and is not even "typically polychaetous." In the lecithotrophic polychaete larvae that develop from yolky eggs (Thorson, 1946), especially in

the bottom-dwelling forms, the gut becomes pervious tardily, for example, on the 10th to 14th day in *Clymenella torquata* (Newell, 1951), which gastrulates 24 hours after fertilization. The echiuroid larva is an annelidan trochophore with two protonephridia.

In my opinion the Echiuroidea are degenerate forms derived from the Annelida. The variability of the preanal setae, the reduced (*Bonellia*, *Bonelliopsis*) or excessively numerous (*Heteromyota*) nephridia, the absence of a compact gonad and a circulatory system in *Urechis caupo*, and the degenerate males of *Bonellia*, suggest regression, not primitivity.

Pocobius, the supposed "connecting link" between the Annelida and Echiuroidea (Heath, 1930), was shown by Pickford (1947a) to be an aberrant polychaete.

The affinities with the annelids of the already mentioned Sipunculoidea, grouped in the coelomate Spiralia, are remote. Annelidan features are the interradial cross in the embryo and some isolated characters, such as the presence of a nuchal organ (Polychaeta), chloragogue tissue on the coelomic surface of the intestine, and haemerythrin as a respiratory pigment (*Magelona*). Of these characters only the cross has phylogenetic value. The so-called molluscan characters in sipunculoid development are not significant (Pickford, 1947c). Their trochophoroid larva differs from the annelidan trochophore in its aberrant prototroch and possession of metanephridia. The primordium of the nerve cord is not annelidan, being unpaired. The circular, oblique, and longitudinal muscles of the body wall, metanephridia, and some other characters are incompatible with annelidan characters but are not specific. In some species the coelom is chambered by incomplete ventral peritoneal folds similar to annelid dissepiments; but these can hardly be viewed as segmental limits, inasmuch as the gut forms a loop bringing the anus near the mouth.

The sipunculoids are probably non-segmented worms. At the anterior end there is a circumoral canal lined with coelomic endothelium; and this communicates with the cavities of the ciliated tentacles and contains coelomic corpuscles. The relations here recall the mesocoel of the Tentaculata; but as the development is unknown, it is uncertain that this canal is a mesocoel. If it really is so, the Sipunculoidea must be considered as lower Spiralia and placed on the line between the Tentaculata and those Spiralia with deutometameres (Mollusca). Nephridia functioning also as gonoducts would be consistent with such an ancestral position. The reduction of the vascular system necessitates regarding the Sipunculoidea as a side-branch, not as direct forerunners of annelids and mollusks.

The Priapulida, already mentioned, are externally similar to the Kinorhyncha, because of the invaginable spiny anterior end. The epidermal position of the ventral nerve cord is also seen in the Kinorhyncha and Nematomorpha, but a lobed brain and segmentally disposed ganglia are peculiar to the Kinorhyncha. Other characters justifying the placing of the Priapulida near or even within the Aschelminthes were indicated by Hyman (1951b). I agree with her that the Priapulida are not derivable from any particular aschelminth class.

ARTICULATA—PARATHROPODA

Three groups, not a natural phylum (sometimes called Oncopoda, or Pararthropoda), bridge the gap between the Annelida, with non-articulated parapodia, and the Arthropoda, with articulated appendages. These three groups are the Pentastomida, Onychophora, and Tardigrada. They have unjoined limbs that terminate in adnate claws, without imbedded bristles. In all three groups, the limbs grow out before the claws develop, contrary to polychaetes, where cirri and bristle pouches are formed first and are then carried outward on an outgrowth of body wall (Snodgrass, 1938). The cuticle, chitinous in pentastomids and onychophores, is molted in these, as also in tardigrades.

The pentastomids are not merely externally ringed as in some mites (Tetrapodili), but possess numerous segments, as their muscles, nervous system, and sense organs reveal (von Haffner, 1926). Arthropodan characters are their chitinous cuticle, molts, absence of ciliated epithelia, transversely striated muscles, and tubular gonads. Some striated muscles, it is true, occur also in certain polychaetes, and all muscles are striated in *Magelona* (Romieu, 1923). Articulata with numerous segments include the Crustacea, Myriapoda, Onychophora, and Annelida. The first two cannot be ancestral to pentastomids, since they have articulated legs and mouth parts. The more highly developed sense organs and the

locomotory, respiratory, and circulatory systems of the onychophores cannot fairly enter into a comparison with those of the pentastomids, because the latter may be reduced by parasitism. The posterior openings of the gonoducts (anterior in primitive pentastomids), the jaws, the long commissures of the longitudinal nerve cords, and the smooth body-wall muscles of onychophores make them unlikely ancestors of pentastomids. Evidently the latter have evolved from polychaetes, among which the Myzostomida show striking parallelism with pentastomids without their arthropodan characters.

The Onychophora are also descended from the Annelida. A general homology exists between parapodium and articulated arthropodan appendage. The Polychaeta correspond, also in other characters, to the supposed ancestors of the Pararthropoda and Euarthropoda. *Aysheaia*, from the middle Cambrian, and with certainty related to the recent Onychophora, was a marine animal. As the Arthropoda originated from the Annelida probably in precambrian times, the connection of onychophores to annelids should not be imagined in too concrete a manner. Even *Aysheaia*, with terminal mouth and branched antennae, represents a special order, the Protonychophora (Hutchinson, 1930). Annelidan characters of onychophores are: uniform dermic muscle tube constituted of smooth fibers, nephridia in nearly all segments, cilia in nephridia and gonoducts, and vesicular eyes as in the Alciopidae. Also the morphology of the brain is polychaetous, as proto- and deuto-cerebrum are not separated (Hanström, 1935); the cerebral centers and the sympathetic system have features of the Crustacea and Chilopoda.

Arthropodan characters of onychophores are: (1) a dorsal heart that receives the blood from the body cavity by segmental slits, not from veins; (2) walls of coelomic sacs dissolved, and the definitive body cavity formed by confluence of coelomic cavities with the primary body cavity; production by cells of coelomic walls of (a) a horizontal septum that separates a venous blood space (pericardium) from the body cavity; (b) adipose tissue and athrocytes; and (c) walls of inner nephridial vesicles, gonad, and gonoducts originated from coelomic sacs of several segments; and (3) superficial cleavage or, in case of total cleavage, an arthropod-like development.

Peculiar characters are, for instance, the ventral nerves similar to ganglionated cords; tufts of small, neither anastomosing nor branching tracheae; and development of jaws and oral papillae as modified limbs of the first and second postantennal segments, as in the Mandibulata, but assuming different definitive positions. In the Protonychophora the postoral appendages are not yet specialized into jaws and oral papillae.

The small body of a tardigrade consists of a protostomium and five segments. The protostomium lodges the supraesophageal brain; the first segment with the subesophageal ganglion is cephalized and lacks appendages; the following four segments each contain a paired ganglion and bear a pair of legs supplied by it. The nervous system is very like that of polychaetes but has arthropodan features, such as reduction of the podial ganglia, segmental nerves not closed dorsally, and absence (or suppression) of lateral connectives (Hanström, 1928). Similar legs and homologous gonad and definitive body cavity in the Onychophora and Tardigrada (Marcus, 1929) make it possible to unite these two groups as Malacopoda. The Tardigrada can hardly, however, be descended from recent Onychophora. The lack of respiratory, circulatory, and, in the primitive Heterotardigrada, of excretory organs could be understood as reductions that are frequent in small Articulata, and the specialized body muscles as a step of progressive arthropodan evolution. The same holds true for the suppression of cilia, the segmental cuticular plates (Echiniscoidea), and the excretory appendages of the gut (Eutardigrada). The two latter are arthropodan characters that have evolved within the tardigrades. The difficulties of a direct phylogenetic connection between the two "malacopodan" classes lie in the peculiar ventral nerves of onychophores, the different pharynges of the two, and the origin of the entomesoderm in tardigrades. A suctorial muscular pharynx with a Y-shaped lumen occurs in both groups, but is entered in Onychophora by a pair of modified limbs whereas the cuticular structures of the Tardigrada are produced by the pharyngeal epithelium. The myoepithelial cells of the tardigrade pharynx recall the Aschelminthes. The enterocoelous development of the coelomic sacs in tardigrades is very isolated among the Protostomia.

An independent but adjacent origin of the

Onychophora and Tardigrada from the Annelida must be assumed.

ARTICULATA—EUARTHROPODA

In the lower Cambrian the Euarthropoda appear with a well-established, stable group (Störmer, 1944), the Trilobita, that already then comprised several lines. Their head bore faceted eyes and one pair of preoral antennae. The appendages of the four postoral cephalic segments as well as those of the following ones are all rather uniform gilled legs, that Störmer showed to be cheliceratous, not crustacean. Although evidently near the origin of the Euarthropoda, the Trilobita represent only the root of the Arachnomorpha (Heider, 1913).

From the Trilobita evolved the Merostomata, with two lines, the Xiphosura and their derivative, the extinct Eurypterida. The Merostomata lost the trilobitan antennae. Their first postoral appendages developed as chelicerae and became secondarily preoral. Two further segments were incorporated into the head inherited from trilobites. The Xiphosura are the oldest Chelicerata; they appear (Aglaspida) in the middle Cambrian with at least 6 pairs of anterior abdominal walking legs. The oldest Limulida are Devonian, and the modern genus *Xiphosura* (= *Limulus*) is identified from Jurassic rocks. The ontogeny of *Xiphosura* agrees in a striking manner with the paleontological sequence (Störmer). The Eurypterida (Ordovician to Permian) lived in semi-enclosed lagoons with either unusually high or unusually low salinity; some of them (*Stylonurus*, *Pterygotus*) attained a length of nearly 3 m. The eurypterids had chelicerae and five pairs of uniramous cephalothoracic legs, as well as five pairs of modified abdominal appendages with reproductive and respiratory functions.

The next steps in the evolution of the Chelicerata were the transformation of the gills to book-lungs and, in part, to tracheae; the reduction of the abdominal legs; and the loss of compound eyes, with persistence of only the ocelli of the Merostomata. The mentioned novelties characterize the class Arachnida, that probably originated from eurypterid-like forms. The oldest known arachnids are scorpions from the upper Silurian, probably air-breathing animals with book-lungs (Petrunkevitch, 1949). Since then this order changed very little nor did it develop noteworthy specializations, though the number of recent species is considerable (over 600).

As a mite of a quite modern type appears already in the Devonian and also spiders (with doubtful spinnerets) are known from this era, scorpions must be a primitive side branch of the Arachnida, of which the other orders developed along another line. Their mutual relations are difficult to judge. Shortening by loss of abdominal segments, concentration of ventral ganglia, transformation of the second legs (pedipalpi), movability and immobility of the coxae, evolution of the tracheae, reduction of arteries, and fluctuations in the number of cardiac ostia occur in several orders, hence phylogenetic lines and those of parallel development are mingled.

The greatest number of primitive characters seems to be united in the Pedipalpi (Amblypygi and Uropygi, now separated and the latter split into two orders; Petrunkevitch, 1949), although embryonic abdominal legs have not been found. Related to the Pedipalpi are the Araneae and the archaic, partly reduced Palpigradi. As spinnerets are abdominal legs, spiders are in this respect more primitive than the Pedipalpi. Ricinulei-Acari-Chelonethi form another group of related arachnids. The extraordinary amount of variation in structure and habits of the Acari is, in part, correlated with parasitism. Isolated arachnid orders are the Solifugae, with three free thoracic and ten abdominal segments and very numerous primordia of abdominal legs; and the Opiliones, with masticatory plates on the coxae of the first two walking legs, possibly homologous with the gnathobases of the Merostomata.

The Pantopoda (Pycnogonida) do not in any phase possess the crustacean biramous limbs or the cheliceratous body composed of cephalothorax with six pairs of appendages and abdomen (Marcus, 1940). Therefore they cannot be included in any other arthropod class nor be derived from them, despite their chelicera-like first appendages. The Palaeopantopoda from the lower Devonian are excluded from the Pantopoda by Calman and Gordon (1933) and Hedgpeth (1947). *Palaeoisopus* had eight preabdominal segments, but since recent forms have seven to nine, this point is not phylogenetically important. The appendages of the Palaeopantopoda show the same mixture of crustacean and cheliceratous characters that the recent forms exhibit in their

ontogeny and anatomy. The hind legs of *Palaeoisopus* had eight joints, as in Crustacea, and the other three pairs nine joints, as in recent Pantopoda, Chelicerata, and Trilobita. Cleavage and formation of the germ layers of pantopods (Korschelt, 1936), their sense organs (Hanström, 1926, 1927), innervation of the proboscis (Hanström, 1928), and the occurrence of larvae are crustacean. The larva has the same number of segments as the *Protaspis* stage of trilobites. Brain (Hanström, 1928), gut, skin, appendages, chiefly the two first pairs, chelophores and palps are cheliceratous (Helfer and Schlottke, 1935). This combination of characters can be explained by supposing the origin of the Pantopoda among the Trilobitomorpha. For the family tree of the Pantopoda and an analysis of the polymerous forms I refer to Hedgpeth (1947).

In addition to the Trilobita some other classes belong to the Trilobitomorpha, two of them without distinctly trilobate dorsal shield. There are middle cambrian arthropods with two pairs of antennae (*Marella*) and Notostraca-like carapace (*Burgessia*), with pedunculate eyes projecting from below the carapace and flat cerci (*Waptia*), and others that closely resemble the silurian and devonian ancestors of recent Leptostraca by reason of a nuchal fold, carapace, and other features (*Hymenocaris*, *Protocaris*, etc.). Owing to Störmer's meticulous analysis (1944) of their trilobitan appendages, one can hardly continue to consider them as progenitors of recent Crustacea. But neither do I think that their crustacean traces can be convergences with characters of a quite independent branch of arthropods. I could imagine that they are homoiologies, reminiscences of animals that constituted the common root of the Arachnomorpha and Mandibulata in precambrian times.

The term homoiologous (Plate, 1922) refers to morphologically and physiologically similar structures that have evolved independently in animals phylogenetically related; thus tracheae and faceted eyes have appeared in several independent lines in arthropods.

Perhaps such Protostraca (Heider, 1914) or Protarthropoda (Snodgrass, 1938) were crawling, centipede-like animals with one pair of antennae and all other appendages developed as uniramous walking legs. These were jointed, not merely folded as in the onchyophoran ancestors, and the muscularization of the limbs had proceeded much farther. Also, compound eyes and the restriction of the nephridia to the anterior part of the body, where they later appear as coxal (Xiphosura), antennal and maxillary glands (Crustacea), or labial kidneys (Myriapoda, Apterygota) were characters of the Protostraca. The thickening of the integument had evidently only begun, for a fossilizable exoskeleton appears first in the lower Cambrian, not yet in little altered, precambrian rocks, which contain waterlaid, presumably marine limestones (Moore, Lalicker, and Fisher, 1952). Cuticular folds that protected the anterior part of the body of the Protostraca may be presumed because they occur in Crustacea and Trilobitomorpha. The preservation of protostracan characters in the latter is also revealed by the combination of arachnomorphous and crustacean traces in the Pantopoda, and the knot on the top of the glabella in the Trilobata, homoiologous to the four-celled sense organ of the Phyllopoda and Anaspidiacea (Hanström, 1934).

The first major diversification of the common ancestors of the Euarthropoda gave rise to the trilobitomorph and mandibulate lines. In the former the legs remained primitive, with nearly equal joints, and preserved the ambulatory type, developing a gill only on the precoxa. In the latter the postantennal cephalic appendages specialized into three pairs of mouth parts, i.e., one pair of mandibles and two pairs of maxillae. This mandibulate line bifurcated early into a crustacean and an antennate branch. The former developed an exopodite on the basipodite (trochanter). Onychophora—probably derived from bottom-dwelling polychaetes with yolky eggs, the Protostraca—and the great majority of the Trilobitomorpha crept on and partly swam along the bottom (Störmer, 1944). Walking legs are also preserved in many Crustacea, but in the biramous nature of their natatory appendages they acquired the organization for pelagic life.

The Phyllopoda, especially the Notostraca, are the most primitive crustacean order, which has remained nearly unaltered since the Triassic. From the Notostraca originated the Conchostraca, and from these the Cladocera, which have preserved larval characters. The Anostraca are separated from the Phyllopoda by pedunculate eyes, reduced carapace, and the differing muscles of their phyllopods. The Copepoda,

Branchiura, Mystacocarida, Ascothoracida, and Cirripedia are related by the possession of six thoracic segments and typical biramous legs. The copepods lost their carapace and faceted eyes; the latter were still present in the triassic *Euthycarcinus*. Allusions to spiral cleavage occur in the Cirripedia. The Ostracoda, known since the Ordovician, are a blind side-branch of the smaller Crustacea; their segment number is greatly reduced, they have five to seven pairs of appendages, including antennae; their valves develop by median fission of the carapace already seen in the nauplius. In this last regard they agree with the Cypris larva of the Ascothoracida and Cirripedia, and not with the Conchostraca.

The larger Crustacea (Malacostraca) are not later than the Entomostraca but evolved simultaneously with them; they have primitive abdominal appendages and lateral arteries. For the phylogeny of the Malacostraca I refer to Siewing (1956).

The Antennata must have separated early from the Crustacea, because they cannot be derived from any crustacean order, and primitive homomerous myriapods with uniramous appendages are more ancestral than any crustacean. The first Antennata are Myriapoda, appearing in the upper Silurian. The tracheae of the Antennata must be an innovation, because this subphylum descends from marine Protostraca. Perhaps in the Silurian, or in the lower Devonian, the Antennata divided into three classes, the Chilopoda, the Progoneata, and the insecta; of these the Chilopoda are the most ancestral group. They are homomerous, with seven-jointed primitive legs, with a genital opening on the penultimate segment, with a rather complete arterial system, and with onychophoran, almost annelidan segmentation, etc. A feature peculiar to chilopods is the transformation of the first legs into a pair of poison claws. The Notostigmophora retain compound eyes. They are followed by the Anamorpha, likewise with 15 trunk segments. The Epimorpha, with more numerous segments and tracheal intercommunications near the stigmata, are the most specialized chilopod order.

In the Progoneata the genital opening is anterior, on the third or fourth segment; hence it is impossible to derive the Chilopoda and Insecta from the first progoneate order, the Symphyla. Nevertheless, the latter must come from near the root of the trifurcation, as they unite chilopodan, diplopodan, and apterygote characters. In some details the Symphyla are reduced. Much more reduced are the Pauropoda, without respiratory and circulatory organs. They show incipient segment fusions, a feature that also characterizes the Diplopoda. Posterior to the fifth segment, all segments, except the last, are doubled and have two ganglia and two pairs of legs. As shown by fossils, this strange phenomenon evolved within the Diplopoda. Ontogenetically the double segments arise by incomplete partition of simple segments.

The ancestors of the Insecta must have been opisthogoneate Antennata, i.e., Chilopoda. These ancestors cannot have been the recent Scutigeridae, which have dorsal unpaired stigmata and many-jointed legs, but must have been more primitive forms with symphylan features. Four of the five insect subclasses are primarily wingless; wings evolved within the class. The Thysanura represent an ancestral subclass; they have free maxillae with long palps; epipodites (styli) on the thoracic legs; appendages on all abdominal segments; faceted eyes; labial kidneys; a short germ band; an amnion developed by invagination; an open amniotic cavity; and a medial frontal organ with double cells and a disk-shaped structure, as in Crustacea (Hanström, 1947). On the other hand, the Thysanura also show characters in common with the Pterygota: mouth parts; distinct paranota on all segments; antenna divided into shaft and flagellum and provided with Johnston's organ; a typical number and position of the stigmata; and an orthopteroid ovipositor formed of the eighth and ninth abdominal legs.

The other apterygote subclasses are side-branches from the main line, the Chilopoda–Thysanura–Pterygota. These Diplura, Protura, and Collembola are entognathous (entotrophous). The Diplura show such archaic features as: vestiges of abdominal legs; myriapodan antennae; segmental ovarioles; and absence of embryonic membranes. But their mouth parts are reduced and they lack eyes. The anamerous Protura lack eyes and antennae, have a shortened dorsal vessel, and reduced or no stigmata. They are evidently a degenerated, early subclass. The Collembola are an isolated, successful group with a mixture of archiac features (myriapodan antennae, labial kidneys, hints of total cleavage,

lack of embryonic membranes), reduced characters (number of abdominal segments, respiratory system, the heart in the Sminthuridae), and specialized characters (abdominal appendages, claws, nervous system). Collembola from the middle Devonian are the oldest known fossil insects.

The Pterygota evolved from lepismatoid Thysanura with reduced styli, enlarged prothorax, and on the mesothorax and metathorax paranotal lobes, which were the forerunners of wings. In the upper Carboniferous (middle Pennyslvanian) several lines of winged insects appeared. There were big Palaeodictyoptera, with only slightly differentiated thoracic and abdominal regions and with two pairs of nearly equal wings. Some had small prothoracic wings, besides. Like resting mayflies and dragonflies they raised their wings straight over the back and did not fold them one above the other over the abdomen. Also the ancestors of mayflies, dragonflies with a wing-spread up to 75 cm., grasshoppers, cockroaches, and perhaps Rhynchota (only wings found) lived in the carboniferous forest.

The phylogentic interrelations of the pterygote superorders are very difficult to analyze, because many of these superorders appeared simultaneously, are uniform in their fundamental plans, and are immensely varied in the details of larval and adult structures. The Holometabola, for example, are either traced polyphyletically from different paleozoic ancestors (Weber, 1949) or derived from a common trunk with aquatic larvae provided with abdominal legs (Jeannel, 1949, quoting Martynov, 1938).

The ancestral superorders Ephemeroidea, Libelluloidea, and Perloidea (Plecoptera) are generally placed at the base of the genealogical tree. The first are prometabolous and are the only group of insects that molt complete wings. They are Paleoptera, i.e., their wings are rigid as in the Palaeodictyoptera. The same type of wings occur in the Libelluloidea, but these are archimetabolous like the Plecoptera. Strangely, the oldest groups of insects have aquatic larvae, although their ancestors, the Thysanura and Myriapoda, are terrestrial. As the tracheal gills of these larvae develop, in part, from abdominal legs, one must assume that insects developed an aquatic larval life at a time when the larvae still had abdominal legs. The terrestrial though hygrophilous Embiidina have a common origin with the Plecoptera.

Another group comprises the paurometabolous superorders, the primitive Orthopteroidea and Blattoidea, and the specialized Hemipteroidea (certainly known since the lower Permian), which conquered a wide range of habitats and, unique among insects, even the pelagic (Halobatidae). The Blattoidea include the termites. The Thysanopteroidea are a side-branch of the paurometabolous group, combining an orthopteroid thorax with hemipteroid mouth parts. The origin of the Psocoidea (Copeognatha, Mallophaga, Anoplura) continues obscure; one may suppose a remote relationship with the Blattoidea.

The holometabolous group of superorders comprises about five-sixths of all species of insects. To it belong the Hymenopteroidea, known since jurassic, and perhaps permian, times; the Coleopteroidea, with undoubted permian ancestors; and the Neuropteroidea. The primitive orders of the latter, the Neuroptera and Mecoptera, are found in the Permian. The Diptera (known since the upper Triassic) evolved from the Mecoptera; and near the origin of the Diptera, the Aphaniptera branched from them. The tertiary radiation of the fleas accompanied the evolution of mammals, their principal hosts. The Neuroptera gave rise to a second line that begins with the Trichoptera and proceeds to the Lepidoptera. The latter appear in the Jurassic and evolve parallel with angiosperms; according to other authors, no true moths or butterflies are known earlier than the Eocene.

DEUTEROSTOMIA—HEMICHORDATA

The Deuterostomia are a coherent unit of the Coelomata (Bilateria). They comprise only two main groups: the Coelomopora (Hemichordata and Echinodermata), earlier called the Ambulacralia, and the Chordata. The relationships between these two groups are more evident than those between many phyla of the complex Protostomia. To the greater uniformity of fundamental plan in the Deuterostomia corresponds a much smaller diversification of species, even omitting the top protostomian groups for speciation, the Nematoda and Insecta. The single molluscan class Gastropoda contains more species than all the Deuterostomia together.

The identical plan of construction of the

Enteropneusta and Pterobranchia justifies their union in one phylum Hemichordata (also called Branchiotremata, or Stomochordata). As, in the *Handbuch der Zoologie*, the relationship between the two classes is questioned, I repeat the principal homologies: three body regions, proto-, meso-, and meta-soma, with corresponding coeloms and coelomopores; pharynx with gill slits; heart and cardiac sac; and general lines of the nervous and circulatory systems. A transitory caudal appendage for fixation suggesting that of pterobranchs occurs in the young enteropneust *Saccoglossus* (Burdon-Jones, 1952).

The Enteropneusta are of all Deuterostomia, or even of all archicoelomate phyla, the animals that are most similar to the constructed ancestral coelomate (Heider, 1914). Further, their tornaria larva connects the hemichordates with echinoderms (Heider, 1910, 1912, ff.). Fell (1945), it is true, considers direct development in the echinoderms no less typical than development of the indirect larval type, but in my opinion the embryonic homologies between the primitive hemichordates and the more specialized echinoderms are decisive for considering the indirect development with pelagic larvae as prototypical for the latter, regardless of whether this type occurs in a majority of species or not.

The Pterobranchia are sessile or semi-sessile, hence unlike the coelomate ancestor; notwithstanding, they may be more primitive than the Enteropneusta (Schepotieff, 1908), as the nervous system is more superficial and the gonads are simple. By their sessility and by their budding, a simple coelenterate mode of reproduction that is uncommon in both coelomate lines outside the archicoelomate phyla, the pterobranchs qualify for comparison with the primitive Protostomia. Their tentaculated arms may possibly lead to an understanding of the pentaradiate symmetry of the echinoderms, as will be mentioned below. Generally the left side of the body preponderates in *Rhabdopleura*. The same asymmetry in the two anterior coeloms of echinoderms can therefore be considered as an ancient heritage. This intrinsic phenomenon is still manifest in the Acrania (Heider, 1912). Pterobranchs extend back to the Ordovician as rare fossils (Moore, Lalicker, and Fisher, 1952); *Eocephalodiscus* has been found in the Tremadocian. Pterobranchs are now believed by some persons to be related to the graptolites, of which one order, the Dendroidea, was represented already in the late Cambrian.

DEUTEROSTOMIA—ECHINODERMATA

When in the preceding lines the Deuterostomia were called a more uniform stem than the Protostomia, I had in mind the dipleurula, the constructed ancestor of the echinoderms, and not their fossil and recent classes with their outstanding peculiarities.

The dipleurula (Bather, 1900; Heider, 1912; MacBride, 1914), a humpbacked, vermiform animal with a short ventral side bearing mouth and anus, had paired proto-, meso-, and metacoels originated as in *Saccoglossus pusillus* (Korschelt and Heider, 1909; Dawydoff, 1948). The protocoels (axocoels) opened by dorsal hydropores, but only the left axocoel and its pore persisted. The pore leads to a vesicle, the pulsatile or cardiopericardic vesicle of the Enteropneusta, the madreporic vesicle of echinoderms. The mesocoels (hydrocoels) of the dipleurula extended into anterodorsal tentacles, initially two. Possibly a mesodermal skeleton, perhaps of cartilaginous consistency as in recent enteropneusts, supported the protosoma. The latter may have been used for crawling, as in *Cephalodiscus* and *Atuburia*. In this dipleurula the water-vascular system originated as tentacles, as supposed by Hyman (1955). The described bilateral construction of *Rhabdopleura* occurs in carpoids and cystoids.

In the next evolutionary stage a third, backward arm evolved. The process of its origin may have been similar to that of the initially united inner arms of *Terebratulina*, which begin as a median fold of the outer arms (Heider, 1914). Triradiate structure is exemplified in cystoids and in the development of the aquapharyngeal bulb in holothurians (Dawydoff, 1948, p. 348). The pentamerous radiality evolved by dichotomy of the first pair of arms. Such a forking or branching process is known in crinoids (Hyman, 1955). In most echinoderms this ancient evolutionary process is evidenced by the development of the left hydrocoel in the direction of the number five; often the five lobes of the hydrocoel do not appear simultaneously. Thus ontogeny agrees with fossil records and reveals a gradual acquisition of pentamerism.

The dipleurula fixed itself by the anterior end, corresponding to the creeping protosoma of *Cephalodiscus*. Here lay the sensory organs that

chose a proper place for attachment. In all animals that attach by the anterior end, the mouth must be removed to a new location. Following the pterobranchian preponderance of the left side, mouth and tentacles migrated to the left side. The left hydrocoel became connected with the originally right tentacles, hence substituted for the right hydrocoel. Such *methorisis* is common when ontogeny is combined with metamorphosis (Remane, 1952). The connection of the right tentacles with the left hydrocoel and the rotation of the right side to an aboral position deprived the anterior right coeloms of their function; hence their degeneration is understandable (Hyman, 1955). When the mouth passed to the left, this curved the left hydrocoel, finally into a ring. Therewith also the tentacles assumed a radial symmetry around the mouth. The ensuing processes (Heider, 1912; Dawydoff, 1948) are of greater interest for the understanding of metamorphosis than for phylogeny.

Though Cuénot (1948) thought that the Machaeridia (Ordovician to middle Devonian) were perhaps dipleurulae with thin plates covering a flexible body, this group is best left to specialists. The Machaeridia have also been considered Amphineura Placophora, and some (*Turrilepas*) are still included in the Cirripedia.

As the paleontology of echinoderms does not throw much light on the evolution of the recent classes, it is only summarized here. Eocrinoidea, primitive attached animals with subglobular theca, stem, and free appendages, had radially arranged plates. They may include the ancestral stock of the Cystoidea and perhaps the Crinoidea (Moore, Lalicker, and Fisher, 1952). The Paracrinoidea, also stalked, but without symmetrically arranged plates, are known at present only from the middle Ordovician. The Carpoidea (middle Cambrian to lower Devonian) contain strange animals with a row of 8 to 42 slits, possibly gill slits, on one side and a stalk that served to raise the animal from the bottom or a tail that wriggled the animal forward. Gislén (1930, 1933) compared them to appendicularians and acranites, and tried to reconstruct their anatomy. But as the latter is only a guess, one cannot decide if in fact the Carpoidea are near the root of the Chordata.

An evidently primary triradiate construction, already mentioned, occurs in the Cystoides (middle Ordovician to upper Devonian). They are related to the eocrinoids, paracrinoids, and carpoids, but are not, as formerly believed, the ancient stem from which all stalked and even free-moving echinoderms are descended.

The Blastoidea extend from middle ordovician to upper devonian times and can be derived from the Cystoidea (order Diploporida). They were short-stalked or stalkless and had folds (hydrospires), possibly of respiratory function. Another cystoidean order, the Rhombiferida, not younger than the Diploporida but with more highly developed respiratory structures, can be combined with the very ancient class Edrioasteroidea (lower Cambrian to Mississippian). These globular or disciform animals fastened themselves with the entire aboral surface or were free; they lacked stem and armlike appendages. Their ambulacra differ from those of all other Pelmatozoa in that pores for the passage of the podia occur between the lining plates of the ambulacral grooves (Hyman, 1955). Therefore this class may contain the forerunners of the Eleutherozoa.

The difficulty of tracing the Crinoidea from non-crinoid Pelmatozoa lies in the diversity of the appendages. Those of the non-crinoid classes, the brachioles, have small skeletal pieces, whereas the brachials of the crinoid arms are continuous with the radial plates of the theca. An origin of the Crinoidea from the Eocrinoidea may, however, be supposed. The Crinoidea began in the lower Ordovician and had a very complicated evolution. The plasticity of most of their organs has lead to a speciation surpassing that of all other echinoderm classes. The range in time of most species is very short. Forms with one arm, with a tuft of featherlike appendages, with repeatedly branched arms, or with five solid, petal-like arms occurred. The stalk sometimes resembled a prehensile tail, as in *Cephalodiscus* (Dawydoff, 1948, fig. 110). The subclass Articulata, from the lower Triassic, still has existing representatives; they probably came from the Inadunata or Flexibilia. In the Jurassic stalked Articulata of four different types evolved into comatulid free-swimming forms, and others that became free but preserved the stalk (Gislén, 1930) died out.

All free-living echinoderms had sessile ancestors (Heider, 1913, 1914), but these are not necessarily the same for all eleutherozoan classes. The auricularian larva of the holothurians is closer to the fundamental dipleurulan type than

the other larvae, among which the bipinnaria of the Asteroidea comes nearest to the auricularia. The holothurian doliolaria is much more like that of crinoids than like the doliolaria-like stage of some yolky-egged ophiuroids. The vestibule, its rotation to the anterior end, and the direct transformation of larva into juvenile occur in both crinoids and holothurians. Primitive holothurian characters are the position of the hydropore when retained, that of the gonopore, and the occurrence of a single gonad in the anterior (median) interradius (Hyman, 1955). The insunk water vascular canals and nerves are specialized features. The ossicles are perhaps juvenile retentions (Korschelt, 1936, fig. 544). Axial sinus and axial gland are reduced. The strange habit of holothurians of lying laterally on the bottom is not primary and was probably acquired from ancestors that crept on their oral surface. Undoubted holothurian ossicles are known since the Mississippian; the middle cambrian forms, also *Redoubtia*, are questionable (for literature see Frizzell and Exline, 1955).

Bather (1901) and Mortensen (1928) derive the Holothurioidea from an early stage of Edrioasteroidea while the thecal plates were still small and irregular. Mortensen thinks that the common origin of echinoids and holothurioids from *Stromatocystis*-like ancestors would account well for the affinities undeniably existing between these two classes.

According to Cuénot (1948), the least modified holothurians are the Dendrochirota, with distinct pentamerism and suckered podia. Some shorten the dorsal side, then assuming the shape of a tunicate (*Sphaerothuria*) or a bottle (*Rhopalodina*) with anus, gonopore, and mouth on the end of a long neck. More modified than the Dendrochirota are the Aspidochirota that crawl on their ventral trivium. Characters of these two orders occur in Molpadonia that lack podia. The bilateral Elasipoda, with flattened creeping sole, can possibly be derived from the aspidochirotes. Also the bathypelagic holothurians probably belong to the Elasipoda (Hansen and Madsen, 1956). The vermiform synaptids (Apoda) differ from the other orders (in which the tentacles contain extensions of the radial canals) by the crinoidan origin of their tentacular canals directly from the water ring. The Apoda are probably the oldest holothurians, but are reduced with regard to podia, radial canals, and other characters.

The Asteroidea and Ophiuroidea, both known since the Ordovician, are today well-separated classes. They have, however, a common root in the Somasteroidea (Ordovician to upper Devonian), some of which may have been close to the pelmatozoan, probably edrioasteroidean (*Edrioaster*) ancestors of the sea stars. *Villebrunaster*, for example, probably lived mouth upward, like the Pelmatozoa, or it moved mouth downward but with upturned arms. The echinoid-like plate system of recent Astero-Ophiuroidea is a secondary acquisition, largely absent in old species. With their open ambulacral grooves, the Asteroidea are more primitive than the Ophiuroidea. Also their bipinnaria, not far distant from the primitive auricularia, and metamorphosis in a fixed stage as in crinoids are old features. In the Asterozoa or Stelleroidea, as the astero-ophiuroid combination is called, deviations from the basic five-rayed plan, that is, an increase in arm number, occurs already in the Silurian and Devonian. In asteroids, the Phanerozonia, with conspicuous marginal plates, are certainly the oldest of the recent orders, whereas cryptozonian families with four rows of podia in each ambulacral groove, such as the Asteriidae and Brisingidae, or with nearly echinoid pedicellariae, are considered as specialized.

The metamorphosis of ophiuroids, accomplished in a free-swimming stage, is very similar to that of asteroids. Also some asteroids (for example, the Astropectinidae and Luididae) metamorphose without attaching themselves. In both classes the oral and aboral primordia develop opposite to one another on the surface of the larva. The internal organogenesis is alike in both classes, also. Young ophiuroids pass through an asteroid stage with an aboral marginal buccal shield around the hydropore (Cuénot, 1948, fig. 273).

Early palaeozoic ophiuroids lacked ventral and dorsal shields; these structures appeared first in the Devonian and since then the specialized modern type of brittle stars is known. Despite the lack of intestine and anus the class is the richest in species of recent echinoderms. Its evolutionary lines are difficult to recognize. The species with branched arms pass through a juvenile phase with simple arms. This favors the opinion that the Euryalae are more recent than the Ophiurae, and this is consistent with the development of streptospondylous articulations of the vertebral ossicles in the Eurylae that allow the coiling of the arms. The Streptophiurae (Ophiomyxidae), with simple articulations also permitting coils, may be considered the most primitive family from which basket stars as well as Zy-

gophiura are derived. The latter have zygospondylous articulations, hence the arms can move sidewise only.

The Echinoidea are the most highly specialized echinoderms. They appear in the middle Ordovician; the oldest, *Myriastiches*, is already a true sea urchin. *Bothriocidaris*, of the same age, is not typically echinoid. Mortensen (1928, 1930–1931) considered it a highly specialized offshoot of the Cystoidea Diploporida. In modern systematic reviews (Cuénot, 1948; Hyman, 1955) *Bothriocidaris* appears as a blind offshoot of very early echinoid stock and without phylogenetic importance. Mortensen derives the Echinoidea from cambrian *Stromatocystis*-like Edrioasteridae and considers the Asterozoa as a separate branch evolved from *Edrioaster*-like forms. The ordovician echinoids lacked a lantern of Aristotle; their masticatory plates are comparable with the mouth-angle plates of asteroids and the jaws of ophiuroids. Pedicellariae and peculiar to asteroids and echinoids, plutei to ophiuroids and echinoids.

The differences between the ophiopluteus and the echinopluteus overbalance their similarities (Korschelt, 1936), hence the possession of plutei by these two groups hardly testifies to ancestral relationship. The metamorphosis in Asterozoa and Echinoidea differs from that in Crinoidea and Holothurioidea by only partial resorption of the larval body. The ectodermal invaginations, oral in the Crinoidea, Holothurioidea, and Ophiuroidea (Hyman, 1955, p. 642), lateral in the Echinoidea, are comparable (Korschelt, 1936). Sterols of one type occur in the Ophiuroidea, Echinoidea, and similar ones in the Crinoidea, but of another type in the Asteroidea and Holothurioidea. I think these facts have only a vague phylogenetic significance because phosphocreatine occurs in ophiuroids, echinoids, enteropneusts, and vertebrates. It is impossible that these four groups should be more closely allied than the four eleutherozoan echinoderm classes. I do not believe, as another aspect of chemical evidence, that the presence of chitin is decisive in phylogeny. Summarizing, I am inclined with Bather, Mortensen, and the paleontologists, to consider the Eleutherozoa as derived along three lines, Holothurioidea, Stelleroidea, and Echinoidea, from three different attached Edrioasteroidea.

The oldest sea urchins were Regularia, belonging to the Lepidocentroida, representives of which still exist, mostly as deep-sea relicts. In early devonian times, the Cidaroidea, still present in the recent fauna, split off from the Lepidocentroida. Derived from the latter also is the order Melonechinoidea, beginning and ending in the Mississippian. Two orders, the Aulodonta, to which the Diadematidae belong, and the Stirodonta, of which the Arbaciidae are the most familiar members, evolved from cidaroids in the Triassic. The Camarodonta stand morphologically close to the Stirodonta; they appeared in the Jurassic and contain, among others, the Toxopneustidae, Echinidae, and Paracentrotidae.

The irregular Echinoidea that pass through a regular stage in their ontogeny appear in the lower Jurassic. The Holectypoida begin with primitive forms that still resemble Regularia, presumably originating from the Aulodonta. The Cassiduloida, also mostly extinct, develop a jaw system that mostly degenerates before maturity. They originated at the same time as the holectypoids, perhaps from the stirodonts. Primitive cassiduloids are intermediate between holectypoids and the frequently burrowing, highly specialized spatangoids (Pourtalesiidae, Loveniidae, Brissidae, and others) that appear in the lower Cretaceous. The youngest order, appearing in the upper Cretaceous, the Clypeastroida, or sand dollars, evolved from the holectypoids.

UNCERTAIN PHYLA—CHAETOGNATHA, POGONOPHORA

As a kind of appendix to those coelomates with protosoma, mesosoma, and metasoma, I will discuss two marine phyla, the benthonic tubicolous Pogonophoras and the planctonic Chaetognatha.

The Pogonophora have attracted attention in recent years through the work of Ivanov (1954, 1955) and Jägersten (1956). Their protosoma is small, includes a nervous mass, and carries one to many fringed tentacles; the mesosoma is somewhat larger; and the metasoma is tremendously long, containing in *Siboglinum* a mysterious "endobody." Protosoma and mesosoma are diffusely separated or not at all, mesosoma and metasoma by a definite muscular septum or diaphragm. The unpaired coelom of the protosoma connects to the surface by a pair of nephridial coelomoducts. Mesosoma and metasoma each contain a pair of coelomic sacs. The nervous system, epidermal in position, forms a main mass and a ring in the protosoma and gives off two longitudinal cords. The closed circulatory system consists mainly of two median vessels. The body musculature consists of sub-

epidermal longitudinal fibers. Mouth, anus, and alimentary canal are absent in the known stages without even any vestiges as in certain fertile gutless Naididae and Turbellaria. Which is the dorsal and which the ventral side cannot be determined by the position of the tentacles or of the nerve cord or of the wider of the two median vessels.

Nothing in the pogonophoran organization contradicts a phylogenetic connection with the Hemichordata, perhaps even with a hint at the ancient graptolites. The nerve ring in the protosoma is a primitive feature. Recent work by Ivanov proves that the animals are solitary and complete.

The Chaetognatha have an embolic gastrula and a ventro-terminal blastopore that lies nearly at the hind end of the embryo. The blastopore closes and opposite it, at the anterior end of the embryo, the mouth originates by an ectodermal stomodaeum. The anus opens so late, in the juvenile animal, that only its posteroventral position relates it to the blastopore. The mesoderm originates by two anterolateral folds of the archenteron. The definitive coelomic cavities are one pair of head coeloms and one pair of trunk coeloms. The latter subdivide secondarily into anterior and posterior (tail) coeloms during the postembryonic migration of the genital cells from the splanchnic to the somatic wall. The pair of tentacles on the head of the recent *Spadella* is also seen in the extinct *Amiskwia* (middle Cambrian). The nervous system is polychaetous, the four groups of longitudinal muscles also annelidan. These features and a transitory solidification of the coeloms make it difficult to place the Chaetognatha. However, the embryological data indicate that they are primitive coelomate, unsegmented, probably deuterostomatous animals, of which the two body-regions, head and trunk-tail, are homologous with the mesosoma and metasoma of the Archicoelomata. One must derive them directly from the theoretically constructed coelomate ancestor (Burfield, 1927), but they are simplified as regards protosoma, vessels, and nephridia.

ORIGIN OF THE CHORDATA

The origin of the Chordata is here presumed from ancestors similar to hemichordates. The relations between Chordata and Hemichordata (especially Enteropneusta) are discussed below. Here only the pharyngotremy and the dorsal nervous center are recalled. The Hemichordata and Echinodermata constitute a superphylum Coelomopora which is as natural as the superphylum Articulata. Therefore possible future evidence of the origin of the Chordata from the Carpoidea would by no means be surprising On the other hand, the often-tried derivation of chordates from annelids that are metamerized Protostomia has already encountered insuperable contradictions.

The notochord, derivable from the roof of the gut as a fortified ridge, is a peculiarity of the chordates, as is also the depression of the dorsal skin, which bring not only the nerve cord but sensory and epithelial cells into the interior. The depression includes the blastopore that becomes a communication between gut and neural lumen. As these characters also occur in the Tunicata, these latter must descend from common ancestors with the other chordates.

Chordate ancestors (Hemichordata or Carpoidea) are coelomate animals. The absence of a coelom in the Tunicata, perhaps except for the pericardium, can only be understood as a reduction, not as an ancient, primitive character. Together with the coelom the nephridia disappeared and the circulatory system is restricted to the heart. The absence of a coelom does not reveal whether the first tunicates were free-swimming or sessile forms. Reductions of this sort may occur within the same class as within the free-swimming *Dinophilus* and the sessile *Pectinaria* of the Polychaeta. The substitution of the intestine in the posterior part of the body by a new formation of rectum and anus in the anterior part, suggests a sessile or semi-sessile ancestor. Whether remnants of this stage are represented by the three postoral papillae of the young *Amphioxus* larva (Naef, 1931, quoting Van Wijhe, 1926, 1929) is doubtful, since fully functional larval adhesive organs occur in the Ganoidea, Dipnoi, and Amphibia. As the metamerism of the chordate trunk is fundamentally a subdivision or multiplication of the metacoel, the lack of metamerism in muscles and nerves of the Tunicata must also be judged as secondary.

RELATIONSHIPS WITHIN THE CHORDATA

In my opinion, tunicates diverged from the line that goes from enteropneust (or carpoid) ancestors to the Acrania, as a side branch on a

level when the fundamental chordate characters had already been acquired, while the hemichordate potencies of budding were still retained. The organization of the Tunicata is certainly lower than that of the Acrania but this low state is principally a sign of regressive evolution. This position is better indicated by the contrast Urochordata-Cephalocordata, than by Minot's concept of Atriozoa for tunicates and acraniates. The two groups agree, it is true, in epidermis, gill slits that are horseshoe-shaped during tunicate development, endostyle (retained in larval craniates), and perhaps branchial cavity (homology uncertain). The gonads open to the exterior or into the peribranchial cavity; this latter feature I consider already secondary in hemichordates, because the first coelomates must be imagined with urogenital coelomoducts. With regard to the last, vertebrates are more primitive than all other Deuterostomia.

The Copelata are best understood as persistent ascidian larvae (Heider, 1914; Brien, 1948; and others), not as primitive tunicates (Lohmann, 1933). The ontogeny is ascidian but accelerated with regard to gastrulation and hatching of an incomplete larva. The general morphology is partly simplified (gills and endostyle), in part specialized (rotation of the tail; caudal muscles and nerves; test). The Oikopleuridae are most similar to ascidian larvae, followed by the Fritillariidae. The Kowalewskaiidae are the most remote from ascidian larvae, having a complicated pharynx, but lacking endostyle, esophagus, and heart. *Oesia* from the middle Cambrian is probably an *Oikopleura*-like appendicularian.

The evolution of the Ascidiacea is characterized by the progressive elongation of the branchial chamber and the complication of its walls by fold and blood spaces. Concomitantly the regionation of the body into two or three parts (Aplousobranchiata) disappears. The originally unpaired mediodorsal gonads shift their position in or behind the intestinal loop (Aplousobranchiata), to one side of the gut (Phleobranchiata), and finally to both sides of the enormous branchial chamber that occupies the whole body length (Stolidobranchiata). The most primitive order contains no solitary ascidians. The aberrant Octacnemida presumably originate in one of the two first orders.

The pelagic ecaudate tunicates, the Pyrosomidea, that are colonies of ascidians, and the more specialized Doliolidea and Salpidea, are united as the class Thaliacea by Brien (1948). He regards them as representing three morphological steps of regressive development of the branchiae, brought about by dislocation of the atrial cavity that assumes a position opposite the pharynx. Budding is essentially similar in the three orders. Brien considers them not as derived from one another but as evolved from a common ancestor in the aplousobranchiate family Polycitoridae.

The Acrania are nearer to the predecessors of the Chordata than are the Tunicata and have only a few secondary characters, among which is the cerebral vesicle with at most two pairs of nerves. Although this vesicle does not show reduction during ontogeny (von Ubisch, 1937), it must be qualified as degenerated when compared with the tunicate brain. Tunicate larvae and the Copelata have a differentiated sensorial archencephalon and a mostly motor deutencephalon. As an evolution from acraniates to tunicates and then to craniates cannot be imagined, the common ancestor of the Chordata must have had a more differentiated brain than do the present acraniates. Possibly the notochord extends in advance of the nervous tube because the brain has become reduced. A further reduction concerning the excretory organs appears possible. Presumably the ancestors of the chordates had open metanephridia, as is assumed for the first Bilateria. Their funnels were lost in the Acrania, whose nephridia thereupon became protonephridia without genital function; the germ cells are then freed by dehiscence of the atrial wall. Even if the solenocytic nephridia of acraniates were primary, and not reduced, organs, it does not necessarily follow that the Acrania are related to worms that have protonephridia. Ciliated cells with excretory function occur in the renal and atrial epithelium of *Branchiostoma*. An increased growth of these patches is conceivable; and when the nephridial surface enlarged, the ciliated cells sank into the subchordal (epibranchial) coelom. In such a manner a protonephridium with solenocytes may have evolved in widely separated groups (Meyer, 1926; Gislén, 1930).

Primitive chracters of the Acrania are: nonstratified, initially ciliated epidermis; absence of skull, limbs, and specialized muscles; absence of a heart; primitive eyes in the spinal cord; dorsal and ventral spinal nerves not united; ciliated gut; endostyle; liver as a hollow outpushing of the gut; separate openings of the nephridia; typical invaginate gastrula; completely separated enterocoelic mesodermal pouches.

Some characters of the Acrania suggest an evolution of the Chordata from the Hemichordata: asymmetry in the formation of somites, head cavities, gill slits, mouth, etc. (Ptero-

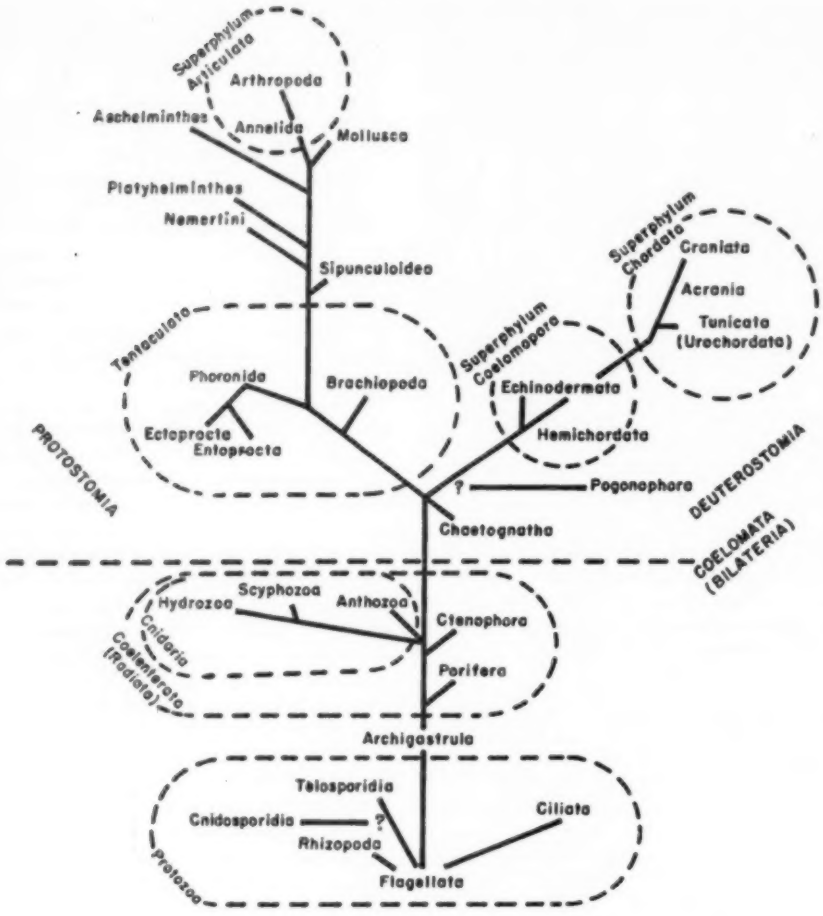

FIG. 1

branchia); respiratory pharynx, development and structure of the gill clefts (Enteropneusta); formation of the anterior somites and their pores as expounded by MacBride (1898, 1900); topography of branchial, genital, and hepatic regions; and possible homology of the anterior end of the nerve tube, with the dorsal collar cord sometimes containing a central canal.

The homology of the stomochord with the anterior end of the notochord is questionable (Heider, 1910). The peribranchial cavity develops from different regions in the Tunicata and Acrania; hence the homology of this cavity in the two groups cannot be established (Drach, 1948). However, a homoiology cannot be denied, in my opinion (Korschelt, 1936). More interesting than the phylogenetic value of analogous organs in the chordate groups evolved from the same root is van der Horst's (1936) interpretation of larval peribranchial primordia in *Planctosphaera*. As the adult enteropneust of which this is presumably an aberrant tornaria larva remains unknown, its possession of a peribranchial cavity cannot be verified and the structure may be transitory. During early stages of development the gonads of *Branchiostoma* lie, as in the Enteropneusta, between the gill slits, opposite the branchial septa. The concomitance of branch-

iomerism and gonomerism in some enteropneusts (van der Horst, 1930) bridges to a certain degree the gap between the Acrania with metamerized, and the Hemichrodata with non-metamerized trunk (metasoma).

Certainly it would be premature to conclude anything from the observation that the Vertebrata, Acrania, Hemichrodata, and some Echinodermata have creatine phosphate as a phosphorus carrier, a compound that does not occur in other invertebrates (Baldwin, 1940; Dawydoff, 1948; Hyman, 1955).

A common root of the Chordata can be admitted. The distance between the Acrania and Craniata is smaller than that between either of them and the Urochordata (Tunicata). This is further evidenced by the upper silurian agnathous fossil *Jamoytius* (Drach, 1948), with well-developed eyes but with many characters of the Acrania.

The evolution of the Craniata is beyond the limits of this article.

The accompanying diagram (see Fig. 1) illustrates the main phylogenetic connections here expounded, although perhaps in too concrete a manner.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will occasionally appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to H. B. Glass, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *Department of Biology, The Johns Hopkins University, Baltimore 18, Maryland, U. S. A.*

LIGHT ON LIGHT

BY JOHN BUCK

National Institutes of Health

A Review of A HISTORY OF LUMINESCENCE *from the Earliest Times until 1900. Mem. Amer. philos. Soc., Vol. 44.*

By E. Newton Harvey. The American Philosophical Society, Philadelphia. $6.00. xxiii + 692 pp. + 50 pl. 1957.

Five years ago, when *Bioluminescence* appeared, one could reasonably have regarded that book both as the last word on the subject and as a fitting climax to a distinguished research career begun just forty years earlier. Yet now with this new book E. Newton Harvey has given us a rich new insight into both biological and inorganic light-production. As in previous books *The Nature of Animal Light*, 1920; *Living Light*, 1940; and *Bioluminescence*, 1952, the author considers the chemiluminescences occurring in living organisms to be akin not only to inorganic chemiluminescences but to a variety of physical processes which result in cold light. Whether lack of heat is actually more than a superficial link between, for example, enzymatic photogeny, frictional luminescence, the light from electrified gases, and the reradiation of energy derived from ultraviolet rays, cathode rays or x-rays, seems open to some question, but there can be no doubt that the association of these varied phenomena is valid from the developmental viewpoint. As Professor Harvey shows, many centuries passed in which no clear distinction was made even between organic and atmospheric light production, and many more before the various species of inorganic luminescences began to be individually recognized.

In the book, which is strictly chronological throughout, students of the history of science in general will encounter many familiar landmarks—Lucretius' atoms; the elementary fire, air, earth, and water of the Greeks; alchemy and the philosophers' stone; the pharmacopeia-by-intuition (which prescribed, at various times, powdered fireflies, lignum nephriticum, and phosphorus for kidney stone); phlogiston; spontaneous generation; and so on. The account begins with 6 chapters (250 pages) surveying the knowledge of luminescence from the times of the Ancients through the Middle Ages and Renaissance to the start of the twentieth century. In this section we first meet some of the luminescences which have been of continuing interest during the long course of recorded observation: the "phosphorescence" of the summer sea; the sparkle of gems; the glow of the mercury barometer; the shining of dead wood, fish, and meat; the aurora; fluorescent minerals; phosphorus; static discharges, as seen in stroked cat fur, will-o-the-wisp, or St. Elmo's fire; the glow-worm and firefly. Here also we meet the men who recorded their observations, wonder, and speculations about such mysteries. Of these, Aristotle, Albertus Magnus, Gesner, Francis Bacon, Kircher, Bartholin, Boyle, Lémery, Hauksbee, Beccari, Spallanzani, Dessaignes, Macartney, Heinrich, Grotthus, Becquerel, Panceri, Stokes, Crookes, Ehrenberg, and Dubois made perhaps the greatest personal contributions, but on the roster we find also an extraordinary number of names famous primarily for other work: Galilei, Descartes, Leibnitz, Newton, Hooke, Réaumur, Halley, von Guericke, Franklin, Lavoisier, Priestley, Davy, Humboldt, Faraday, Darwin, and Herschel, for example.

The clue to the fascination exerted by luminescences is that, during most of the period surveyed, workers were less concerned in how or why a given object luminesced than in the nature of light itself. From the vantage point of Twentieth Century sophistication it is difficult for us to hark back to times when emission was not distinguished from reflection, when friction was misunderstood, when color was an enigma, when incandescence and phosphorescence were hazily related, when invisible radiation was unthinkable, when a bar-

ium sulphate spar—the famous Bolognian phosphor—was conceived of as a sponge which soaked up "luminous fluid" by day and gave it back by night, and when even the ocean was thought to act as such a "light magnet." These were conditions under which all men of inquiring mind could find in light—and in the equally mysterious and inextricably associated heat and electricity—a natural, striking, varied, universal, and altogether irresistible common ground for exploration. Thus in the 205 pages of Part II (Luminescence in Non-living Material) we follow the slow and painful emergence of the physical and chemical principles necessary for sorting out and studying the species of inorganic cold light: phosphorescence, electroluminescence, fluorescence, radioluminescence, thermoluminescence, chemiluminescence, and so on. Similarly, in the third and final section of the book (140 pages) we find the biologists struggling, on the one hand, to acquire the essential anatomical and physiological knowledge of their materials, and on the other to correlate bioluminescent phenomena with advances in the physical sciences. In this connection, though the *History* has formal time limits ("From the earliest times until 1900"), one could wish that Harvey had included a few summary paragraphs on the present status of each type of luminescence. It is something of a disappointment to follow an increasingly hot scent only to have it peter out in statements such as "A great deal of research has been carried out in this field in the twentieth century," or "Their work has formed the basis for present theories of phosphorescence."

This vista of science in progress is not achieved without effort by the reader, for he has to contend with Harvey's meticulous documentation and with the repetitions imposed by the complexity of the subject and the interlocking organization of the book. This is a comprehensive treatment, and a critical one, containing no snap judgments or cursory surveys. Some 1600 names are listed in the Author Index, all of which are at least mentioned in the account at the appropriate dates, and at least half of which receive more than passing mention—ranging up to several pages. The 70-page bibliography lists nearly 2000 books, monographs, journal papers, tracts—and that vanished symptom of scholarship, the prize essay—each of which is cited at least once, if not in the text at least in one of the book's 790 footnotes. Each writer who has been sufficiently interested in a luminescence to accord it space in monograph, textbook, or encyclopedia is given his due, even if his statements add nothing to those of ten contemporaries, or even represent a backward step. An important worker may come up for consideration several times, as we learn first of his general significance in the field and then follow his specific opinions and experiments in relation to several types of luminescence. One is constantly impressed with the author's tenacity and industry in sorting out and cross-indexing the almost overwhelming mass of detail, and this with virtually no typographical errors or frank duplications. One is impressed also with his success in relieving the tedium of cataloging by sidelights on man and times. For example, almost every worker is at least identified—"A court apothecary to Louis XIV and son of an apothecary . . .," ". . . a benedictine monk at the Royal Monastery of St. Emmeran . . .", "at various times professor of medicine, physik, botany, anatomy and surgery at the University of Jena . . .," ". . . a banker and mayor of Warsaw . . .," and often his career and interests are given in considerable detail, with explanatory notes upon contemporary political and scientific conditions. Interest is enhanced also by 44 full-page plates of frontispieces and illustrations from the most important works on luminescence and light. And—most helpful of all—Harvey has, wherever possible, let the story unfold in the observer's own words. These numerous and full quotations—by turns quaint, obscure, charming, penetrating, ridiculous—do more than anything else to liven the history and supply the atmospheric background, and in mass they form a truly fascinating commentary on science in general.

The reader of this book, then, reaps two major rewards aside from specific information. First, in seeing the pageant through contemporary eyes, rather than by modern hindsight, and in being forced to consider both the sense and the nonsense of the era, he experiences scientific development as the slow, tantalizing, and often comic process that it is, rather than as the facile progression it seems to be in superficial accounts. He has a box seat at a contest starring all-but-blindfolded actors. Time after time he sees the prize missed by reason of superstition, prejudice, or established authority, or because of the imperfections of primitive apparatus, or for lack of simple scraps of information such as the existence of invisible types of light, of microscopic organisms, of colors in white light, of several species of "air," of molecules, atoms or electrons. Second, the reader glimpses science of a degree of freshness and mystery forever lost to us of the twentieth century, smothering as we are in a torrent of printed knowledge, backed into some tiny corner of esotericism, and at grips with our small problems only through the mediation of roomfuls of equipment. He sees inquiry burgeoning under the explosive impacts of the experimental method and an unlimited horizon, and he experiences some of the excitement which led men of so many walks into scientific recreation and which must have made the sessions of the Royal Society and French Academy, with their "live" experiments, so much more stimulating than modern paper-reading.

Finally, the appearance of *A History of Luminescence* is an outstanding event from two further points of view. First, as a work of pure scholarship, its publication is in the best tradition of learned societies, and the

American Philosophical Society is to be congratulated on having issued such a memoir, particularly at a price that must be well below cost for such an excellently manufactured volume. Second, in conjunction with Professor Harvey's earlier books, it marks one of the very rare occasions when a single individual has been able to comprehend the whole of an important and active field of scientific endeavor and present it in a definitive way. It is a tribute to "Mr. Bioluminescence" that he has accomplished this task of a lifetime while maintaining broad biological interests in both teaching and research.

REVIEWS AND BRIEF NOTICES

GENERAL BIOLOGY: PHILOSOPHY AND EDUCATION

UNESCO SOURCE BOOK FOR SCIENCE TEACHING.
United Nations Educational, Scientific and Cultural Organization, Paris; [Columbia University Press, New York.] $3.00. 222 pp.; ill. 1956.

The purpose of this excellent book is to improve science instruction in schools and teacher-training colleges, by basing it on observation and experiments rather than on just the reading of some textbook. The *Source Book* will be an invaluable aid to a classroom teacher who is confronted with the need of teaching science without having had specialized training in this field and without science laboratory facilities.

In the introduction, the book gives a very complete list of simple equipment which will be needed for the experiments described in the book. Much of it is inexpensive and easily obtainable. Chapter 1 deals concisely, in an excellent, practical manner, with the philosophy of elementary science teaching, its methods, approach, resources, and facilities. Chapter 2 gives clear directions for the construction of pieces of general equipment. If these directions are followed, many other ideas will suggest themselves for equipping a simple elementary science laboratory in the classroom, where boys and girls will get the thrill of making their own "scientific discoveries." Chapters 3 through 17 list approximately 750 basic experiments grouped under the following headings: plant study, animal study, study of rocks, soils, minerals and fossils, astronomy, air and air pressure, weather, water, machines, forces and inertia, sound, heat, magnetism, electricity, light, and the human body. Chapter 18 gives much helpful information, such as the proper way of cleaning glassware, how to kill insects, how to make a blueprint, how a hand lens should be held, etc. The appendix contains tables of weights and measures, stars and planets, elements, densities, heat constants, relative humidity, and much other valuable information.

Diagrams of apparatus and directions for doing the experiments are easy to follow. Experiments are chosen in such a way that they show the basic principles clearly and are simple enough so that the experimenter is almost certain to succeed.

The purpose of this volume is not to replace the textbooks, but rather to provide meaningful and abundant science experiences for boys and girls which would send them to their textbooks for explanations and further information. For that reason, the principles involved in the experiments are stated very briefly. Two minor disadvantages of the book are its lack of an index and, for American school children, the use of the metric system throughout. However, the headings of the chapters and the illustrations are so clear that there should be no difficulty in using this book. As to the use of the metric system, it also should present no real difficulty, since conversion constants are given in the appendix. This book belongs in every elementary and junior high school classroom.

MARY DEMEREC

WORKING WITH CHILDREN IN SCIENCE.
By Clark Hubler. Houghton Mifflin Company, Boston. $5.50. viii + 425 pp.; ill. 1957.

In introducing science into the elementary schools, Hubler states that a good program must keep children's natural intellectual curiosity alive, must arouse interest in further study, and must promote basic literacy in science in the growing generation. He believes that these aims can be attained only by allowing children to learn through their own investigation and experimentation.

Such a program would serve the needs both of future scientists and of non-scientists.

The first part of the book is devoted to an interesting and practical discussion of problems which a teacher is likely to encounter in trying to introduce such a program into a classroom. The author offers suggestions how work can be initiated, how scientific concepts can be developed, and how it is possible to utilize children's ideas and interests and still keep the program coherent. The scientific approach and the scientific way of working are clearly explained, the desired outcomes are listed, and the utilization of science material in teaching basic elementary school subjects, reading and writing, is illustrated. The author gives a good list of necessary equipment and materials, and places where these can be obtained. He deals realistically with the problem of storage. He points out that the introduction of a program of this type needs help from the administrative staff of the school in the practical matter of providing equipment and materials and in keeping the school program flexible.

The second half of the book describes interesting activities for children in the following fields of science: the sky, rocks and soil, living things, magnetism and electricity, air and weather, machinery, and sound. All of the information necessary for carrying out the activities is given, as well as a brief explanation of the scientific principles involved. Due to the size of the book, the number of activities is limited, but a good bibliography is included to enable the teacher to carry the subject further.

MARY DEMEREC

SCIENCE IN THE MAKING.

By Joel H. Hildebrand. Columbia University Press, New York. $3.00. 116 pp.; ill. 1957.

In this slender volume, Joel H. Hildebrand, a chemist of international repute, attempts to convey to the general reader something of the philosophy of the scientist and the means whereby he follows his calling. The occasion is the delivery of the Bampton Lectures in 1956 at Columbia University, and the author chose to illustrate his points by taking the listener (or the reader) along with him, step by step, as he worked out a logical theory of solubility. The travelogue should clearly convince his audience that there is no certain path to truth, and that truth is more nearly an approximation than a finality. Hildebrand also speaks on the subject of the increasing specialization of scientists. He recognizes its dangers and its advantages as well as its obvious necessity, and concludes by considering the special role of the scientist in the acquisition of knowledge and power. Along the route the flabbiness of our educational system is discussed and denounced.

The volume is an uneven one. The author is at his best when dealing with his own subject, chemistry; the other topics have been dealt with more tellingly by many others.

C. P. SWANSON

MYSTERIES OF SCIENCE. *A Study of the Limitations of the Scientific Method.*

By John Rowland. Philosophical Library, New York. $6.00. ix + 214 pp. 1957.

The reading of this small book carried me back to my childhood, when I listened to heated discussions between my father and some of his contemporaries on science and religion, my father defending the agnostic point of view. I also remember a book on my father's shelves entitled, *Conflict of Religion and Science. Mysteries of Science* is to me merely a continuation of those discussions, but the argument points in a different direction from that of fifty years ago. Then agnosticism proclaimed, at least within my hearing, that science eventually would explain all the mysteries of the universe, whereas Rowland is of the opinion that some of its mysteries will never be explained and are not susceptible of scientific explanation.

The text leads us through summaries of the scientific accomplishments of physics, biology, psychology, and sociology. In a part called "the unclassifiable," phenomena such as mental telepathy, "dowsing," and flying saucers are discussed. The objective in each summary is to emphasize the limitations of each discipline in regard to its ability to solve all of the problems with which it deals. The author reiterates time and again that science explains the "how" of the universe but never the "why." I have the feeling that he has convinced himself against his will that there is a God, a supreme ruler of the universe, who has endowed man alone with the power to reason and the spark of conscience; and that religion is an essential part of life itself.

The foreword of the book consists of a letter to the Reverend Sidney Spencer, Principal of Manchester College, Oxford. The last paragraph may be quoted as the conclusion of the author's reasoning: "My contention is that, until Scientists in general come to see the limitation of their own subject, disputes will continue and the division of human interest between science and religion will, in a sense, split human life in half. If this book does something to heal that breach I shall have been well repaid for writing it."

H. HANFORD HOPKINS

BIOLOGY: HISTORY AND BIOGRAPHY

JOHN MUIR, *Father of our National Parks.*

By Charles Norman. Julian Messner, New York. $2.95. 191 pp. 1957.

John Muir, who was born in Scotland in 1838 and who

died in California in 1914, was a great naturalist and explorer. He could also write well, and people—even important people—read what he wrote. Thus, almost automatically, he became a leader in the fight to preserve our natural resources from those who would destroy them by the crude methods of exploitation then in vogue. John Muir did much to make his fellow citizens aware of the wealth of natural wonders that they possessed, and, as much as any other individual, he was responsible for the Yosemite's becoming a national park. Indeed, our whole natural park system owes a great deal to his untiring efforts.

This is a very clearly written and sympathetic biography. It not only recounts the events and instances of Muir's life, it also depicts something of the spirit of his outdoor living. The author obviously has much of the feeling for nature that John Muir had himself.

CONWAY ZIRKLE

EDWARD PALMER. *Plant Explorer of the American West.*

By Rogers McVaugh. University of Oklahoma Press, Norman. $6.00. xvii + 430 pp. + 15 pl. 1956.

Edward Palmer (1831–1911) was a great botanical collector but not really a botanist. He was an "original," an eccentric, humorless, and quarrelsome man who was not especially interested in plants, unless they had some ethnological importance. He was also an anthropological collector, who once even tried to add a recently killed Indian baby to his collection and was disgusted when the baby's relatives buried it secretly where he could not find the grave. Palmer apparently just liked to travel, and was quite willing to collect whatever he could sell in order to pay his traveling expenses. His collections, nonetheless, were very extensive and excellent, and now they are of great taxonomic importance.

Palmer's biography constitutes only a fraction of this book (122 pages). It is followed by a detailed geographic index of his collections (240 pages) and five appendices (47 pages). Rogers McVaugh has really written two books in one. The first is an interesting biography of an exceptionally human and colorful character. The second is a compilation of technical facts important for his fellow systematists. The work is detailed, but the details are well organized and subordinated to the whole. The biographical portion should be of interest to many persons, primarily because (1) Palmer himself had no sense of humor; and (2) McVaugh has.

CONWAY ZIRKLE

CLASSICS IN ARTERIAL HYPERTENSION. *American Lecture Series, Publ. 290.*

By Arthur Ruskin. Charles C Thomas, Springfield, Ill. $9.50. xxv + 358 pp.; ill. 1956.

This book is divided into two main sections: the first considers the major contributions to methods of measuring arterial pressure. The initial discussion of these concerns the many experiments of Stephen Hales (1733) in his *Statical Essays containing Haemastaticks; or an account of some Hydraulick and Hydrostatical Experiments made on the Blood and Blood Vessels of Animals.* In Experiment I, Hales measured arterial pressure in a mare by using brass pipe connections and a glass tube. He subsequently measured pressure changes during exsanguination, and later the capacity and shape of the ventricle was determined from a wax mold. In Experiment IX Hales considered the effect of the capillary bed on arterial pressure and from his measurements in the mesenteric vessels concluded: "For tho the velocity of the blood at its first entrance into the aorta, depends on the proportion the area of its orifice bears to the quantity thrown into it at each systole, and also on the number of those systoles in a given time: yet the real force of the blood in the arteries, depends on the proportion which the quantity of blood thrown out to the left ventricle in a given time, bears to the quantity which can pass thro the capillary arteries into the veins, in that time."

Poiseuille measured pressures with a U-tube mercury manometer attached to an artery, with sodium bicarbonate solution intervening to prevent coagulation. Ludwig shortly thereafter added a float which permitted kymographic recordings of pressure during the phases of respiration. Riva-Rocci used an arm cuff to measure arterial pressure by palpation, and Korotkov modified this by using auscultation.

The larger part of the book is concerned with the significance of arterial hypertension and particularly with its consequences, in the form of apoplexy. Beginning with a brief description by Caelius Aurelianus, Ruskin rapidly turns to more recent times to consider the postmortem examinations by Wepfer in 1658, who described cerebral hemorrhages. A brief discussion of the kidney and of hypertension is introduced by a few case reports of Richard Bright, followed by the observations of Johnson, Traube, and Gull. That hypertension may precede renal disease was suggested by Mahomed in 1874. Potain advanced the idea of a generalized, rather than a renal, origin of hypertension and related hypertrophy of the heart to this. Gower's description of the "State of the Arteries in Bright's Disease" is also briefly included.

Finally, the last fifty years of investigations are included with (a) the discovery of renin; (b) the effect of intracranial pressure on the vasomotor control of pressure; (c) the control of the four carotid sinus and aorta depressor nerves on arterial pressure; and (d) the recent experiments on unilateral hypertension.

The introduction is devoted to the very early de-

scription of the pulse from the Yellow Emperor's classic of internal medicine. How many physicians still believe that "nothing surpasses the examination of the pulse, for with it errors cannot be committed"?

This book is very readable and certainly well written. It should be instructive to medical students and physiologists, and physicians will find it enjoyable.

LOUIS K. DIAMOND

THE YOUNG NATURALIST

EXPERIMENTS WITH A MICROSCOPE.

By Nelson F. Beeler and Franklyn M. Branley; illustrated by Anne Marie Jauss. Thomas Y. Crowell Company, New York. $2.75. 154 pp.; ill. 1957.

The book explains simply and clearly how a microscope is constructed and how it works. It gives numerous suggestions as to what to study under the microscope, how to obtain this material, and how to prepare it for microscopic study. The materials suggested meet a variety of interests, are easily available, and are inexpensive.

The reader should have no difficulty in following directions for making his own slides. The book lists reagents used by professional workers, and in addition suggests substitutes which can be found in any home or school. It might have been of help to the younger readers had the authors suggested the optimum magnification for each type of specimen discussed.

This book will appeal to a wide range of readers. The print is large and clear and the language simple and direct, so that much of it could be read and used by alert ten-year-olds. It is a good starting book for older biology students, who will find the chapter on sectioning challenging and helpful. The book will be a valuable aid to teachers of upper elementary and Junior High School grades, who might not have had training in this type of work and would like to obtain some basic information on this subject.

MARY DEMEREC

WALT DISNEY SECRETS OF LIFE. *A True-Life Adventure.*

By Rutherford Platt and the Staff of the Walt Disney Studio; based on the film narration by James Algar. Simon and Schuster, New York. $2.95. 124 pp.; ill. 1957.

To state that *Secrets of Life*, like the other two books in this series, *The Living Desert* and *The Vanishing Prairie*, is based on the Disney nature film of the same name should identify the book to most readers. One sees few natural history photographs as superb as Walt Disney's. The text is based on the narrative of the film and covers the secrets of rocks, soils, flowers, bees, etc. It is simple without being condescending, and is interesting for junior readers. Many ideas are more eloquently expressed than in the usual academic fare. Take this example on the notion of inheritance: "A grain of pollen is invisible to the naked eye. It is only a single cell. Yet into this tiny structure are distilled all the personality and characteristics of the parent plant."

The book should be suitable for ages 7 to 14. It is unfortunate, in a way, that the movie itself is so excellent that, to the reader who has seen it (and it would be unthinkable not to), the book comes definitely as an anticlimax. This was not only my own reaction but also that of the three children who read my copy of the book.

ALAN D. CONGER

ECOLOGY AND NATURAL HISTORY

AGRICULTURAL ECOLOGY.

By Girolamo Azzi. Constable & Company, London; [Essential Books, Fair Lawn, N. J.]. $7.20. xvi + 424 pp. + 6 pl.; text ill. 1956.

AMERICA'S NATURAL RESOURCES.

Edited by Charles H. Callison. The Ronald Press Company, New York. $3.75. v + 211 pp. 1957.

CLIMATE AND ECONOMIC DEVELOPMENT IN THE TROPICS.

By Douglas H. K. Lee Council on Foreign Relations. New York; [Harper & Brothers, New York]. $3.50. xviii + 182 pp.; ill. 1957.

THE FUTURE OF ARID LANDS. *Papers and Recommendations from the International Arid Lands Meetings. Amer. Ass. Adv. Sci. Publ. No. 43.*

Edited by Gilbert F. White. The American Association for the Advancement of Science, Washington. $6.75 (AAAS Members, $5.75). ix + 464 pp.; ill. 1956.

The titles of these books are descriptive enough to require no particular explanation. As a group they symbolize the growing pressure upon soil and space that lurks behind the deceptive camouflage of our present—and local—farm surplus.

Two of the books deal especially with trophic centers —one old, Italy; the other, our own country, new. Two deal with peripheral areas, in so far as cultural development is concerned, namely, the tropics and the arid lands. Both of the latter are not only under steadily increasing economic pressure but also are getting increasing attention, of varying merit. Much of this attention is serious and legitimate, but some of it, one suspects, is a precarious, perhaps even specious, effort to avoid a direct approach to the growing crisis of population pressure and urbanization.

Azzi's book has been translated from the Italian for its value to "agronomist, botanist [and] grower." Callison has edited a series of essays by specialists,

under sponsorship of the Natural Resources Council of America. Lee has organized the results of conferences developed by the Council on Foreign Relations, while White's volume summarizes a world conference underwritten by an imposing group of organizations. These circumstances should remove any lingering doubt as to the importance of the topics dealt with in the group of volumes.

Azzi, professor of agricultural ecology at Perugia, presents many examples of mass quantification of varietal yields in relation to factors of the environmental complex. As a means to this end, he divides the life cycles of crop plants into subperiods, utilizes the velocity-mass-structure concept, and considers yield in both qualitative and quantitative aspects. Productivity and resistance he considers the principal factors in yield. While his work centers largely on a tremendous volume of data from Italy—and none of his references to American work are recent—he has suggestive and informed comments on crop behavior in many parts of the world. It is my judgment that the volume merits serious study, and my impression that the author may be justified in his obvious confidence, but I would be obliged to defer to those more intimately experienced in the field than I am as to its ultimate value.

America's Natural Resources is multi-authored and intended as a concise guide to the renewable or nonmineral resources and the development of a sound public policy with respect to them. The two introductory chapters, one on ecology, the other on population and resources, go directly to the basis of conservation. The chapters on individual resources are by competent specialists and in every instant terminate with concrete suggestions. As an appendix, a national policy is presented, stressing individual responsibility and the need for sound administration. A national board of review to pass on the merits of resource projects in the light of a proper policy is recommended. Certainly some such responsible and intelligent correlating mechanism is long overdue.

Lee's compact volume on the tropics has especial interest as an example of method. Thanks to the energetic interest of Heman Greenwood, the Council on Foreign Relations arranged a series of conferences on problems of the humid tropics, during which a great deal of valuable if inconclusive material was presented. Instead of the usual edited transcripts, Lee was delegated to organize and expertly edit a report. His field experience and professional knowledge of physiological climatology, as well as his appreciation of the extent of the unsolved problems, supply a unity not always evident in conference documents. Along with Bates' *Where Winter Never Comes*, this book gives a realistic notion of tropical potentials that offers promise without feeding the extravagant claims of those who see no limits to the future exploitation of the earth.

White's editorship of *The Future of Arid Lands* has resulted in an attractive and useful volume, issued as No. 43 of the series of publications of the American Association for the Advancement of Science. Water and the adjustments of man, plants, and animals to its limited availability were the obvious themes of the unusually well-organized Arid Lands Meetings in New Mexico in 1955. Thirty-three papers by specialists—many of them eminent—from the several continents and from numerous disciplines are followed by a brief summary and a chapter of conference recommendations. (See also a review in *American Antiquity*, 23: 89–90. 1957.) Essentially these recommendations emphasize the need for sound knowledge as a prelude to action. Prescientific man, using only trial and error, did a better job of utilizing arid lands than is commonly appreciated. But with the power of modern technology any exploitation that is not guided by cautious appraisal and thorough understanding can easily be self-defeating in this delicately balanced and vast portion of the earth's surface.

PAUL B. SEARS

HUNTERS OF THE STORMY SEA.
By Harold McCracken. Doubleday & Company, New York. $4.50. 312 pp. 1957.

This history of the sea otter trade in the North Pacific, more particularly of the Russian American Company, is based for the most part on standard sources. According to the dust jacket, it is "a hard-hitting narrative of a bloody, dramatic chapter in our history," which means, in this case, that it is a reasonably straightforward historical account, couched in swashbuckling prose. The "meek little sea otter," as he is repeatedly called, is only the unwitting central actor in this violent history. The author covers much familiar ground about the sea otter trade but does not cite Adele Ogden's work, although the phrase "Elysium survival sanctuaries of the sea otter" (p. 287) sounds very much like Ogden's "otter Elysium."

The treatment of the California episode is naïve and loose. It is not quite true, for example, to imply that Fort Ross failed primarily because of unsuitable colonists, since the climate there is far from being "sunny" or "salubrious," as the author seems to think. The author misses a golden opportunity to develop the story of the immediate events leading to the purchase of Alaska, centering around the failure of the Atlantic Cable and the Western Union Telegraph Expedition; but he is content to conclude that, had it not been for the "meek little sea otter," Alaska might never have become part of the United States.

There is a brief index, but no formal bibliography. Sources are indicated in a series of terminal notes.

JOEL W. HEDGPETH

CREATURES OF THE DEEP SEA.

By Klaus Günther and Kurt Deckert; translated by E. W. Dickes. Charles Scribner's Sons, New York. $3.95. 222 pp. + 1 pl.; text ill. 1956.

This book was first published in Germany in 1950 as *Wunderweld der Tiefsee.* It has evidently been well received in Europe, since there is also a French translation. As a popular work it is a good general summary of our knowledge of the deep sea and its life and of theories of the origin and evolution of the sea, but events subsequent to its original publication have dated it. It contains no mention, for example, of the bathyscaphe or of the Galathea Expedition. Both of these, of course, were subsequent to the original German edition of the book; but the translation appeared in 1956.

Some passages, such as the description of current-action (p. 69), are too crudely popularized even in the original, while others have suffered from the translation. It is unfortunate that the translation was not read by a specialist, who could have objected to the translation of "Generationswechsel" as "interchange of generations" or to the use of "stem" in reference to the structure of *Vellela.* The translation, incidentally, retains in large part the flavor of the German, even when the result is not always the best English. The reader is asked to ascend such sentences as the following: "On the quantity, however, of the nannoplankton depends that of the rather larger plankton animals that feed on the plant plankton. . . ." The book is profusely illustrated with pen and ink drawings, but those of the crustacea in particular are more spirited than precise.

JOEL W. HEDGPETH

LE PARC NATIONAL DU NIOKOLO-KOBA. *Fascicule 1. Mém. Inst. franç. Afr. noire, No. 48.*

L'Institut Français d'Afrique Noire, Dakar. 1700 fr. (paper). 267 pp. + 14 pl. + 1 folded map; text ill. 1956.

The memoir consists of 17 papers by various authors, chiefly French, based on studies made and material collected in 1955 and 1956 in this, the oldest of the National Parks of French Equatorial Africa. An introductory article gives general ecologic and meteorologic data about the chief types of environments in the Park. The remaining articles are almost entirely systematic, although that on mammals is illustrated by a series of photographs of some of the species taken in the wild, and that on mosquitoes is accompanied by photographs of the habitats of the chief *Anopheles.* Although some of the papers are little more than lists of the species collected, others are much more elaborate, containing lists of bibliographic references, discussions of general distributions, systematic descriptions and, in some cases, figures, descriptions of new species, and occasional ecologic data of general interest. Much of the information is, therefore, of importance to systematic workers in the groups covered. These are: bats (Chiroptera); other mammals, birds, reptiles, amphibians, fish (a short, bare list); Hemiptera; Culicidae and other parasites; butterflies; Myrmeleontidae (Neuroptera); aquatic Coleoptera (Dytiscidae and Haliplidae); Odonata; ticks from mammalian hosts; rhizopod Protozoa; and Infusoria from ruminant mammals.

ALEXANDER B. KLOTS

EXPLORATION DU PARC NATIONAL DE LA GARAMBA. *Ecologie, Biologie et Systematique des Cheiropteres, Fascicule 7.*

By Jacques Verschuren. Institut des Parcs Nationaux du Congo Belge, Bruxelles. B. fr. 900 (paper). 471 pp. + 2 pl. + map; text ill. 1957.

This report is concerned with a study of the bats of the Garamba National Park, a reserve in the northeast corner of the Belgian Congo on the western side of the Congo-Nile watershed. Two years of work were completed in the field as well as several months of study of the collections afterward.

The second part of the report is the most voluminous, and is an excellent taxonomic review of the fauna of the region. Four species of megachiroptera and 34 of microchiroptera, representing altogether 7 families, are reported as occurring within the park. Each one is discussed in considerable detail, often with diagrams illustrating the type of retreat in which the species may be found. For most species a wealth of information is provided, as well as many excellent photographs.

The really notable part of the report, however, is the first part, which deals with the biology and ethology of the bats. The author classifies the diurnal retreats of bats as macrobiotypic (forest galleries, stream border vegetation, etc.) and microbiotypic (cracks in rocks, forks of trees, etc.); and he classifies the bats themselves as phytophilous, lithophilous, or anthropophilous, depending upon their choice of macrobiotype, and external or internal, free or in contact, depending upon their choice of microbiotype. Each of these is illustrated by a simple diagram, and the number of species in each category is presented schematically in a graph. Each habitat is discussed in considerable detail and is well illustrated. It is ipteresting that in no family studied was the ratio of males to females less than 40%, while in the Vespertilionidae it was exactly 50% and in the Megadermidae 58% were males.

In their studies of sociability in the Congo bats, it was found that only 4 species were totally gregarious; the rest were evenly divided between semigregarious and solitary. Only 4 species were found habitually to form interspecific aggregations. A brief discussion of food habits is included, and the section on reproduction includes not only the author's own data, but a literature review as well.

In 14 species anthropic factors seem to have favored the bats, either by providing structures in which they find refuge, by cultivating mango or banana trees or otherwise modifying the vegetative environment. In 15 species anthropic features seemed to be neutral or slightly unfavorable, while in 24 human influence has varied from slightly to strongly detrimental. Deforestation seems to be the main unfavorable factor, brush fires also having some effect.

BRYAN P. GLASS

BIOLOGICAL INVESTIGATIONS IN THE SELVA LACANDONA, CHIAPAS, MEXICO. *Bull. Mus. comp. Zool. Harv. Coll., Vol. 116, No. 4.*

Edited by Raymond A. Paynter, Jr. The Museum of Comparative Zoology at Harvard College, Cambridge. $1.25 (paper). Pp. 193–298; ill. 1957.

The Selva Lacandona is a little-explored forested region of approximately 15,000 square kilometers, bounded on the south and east by Guatemala and separated from central Chiapas by the Río Jatate. The expeditionaries to the Selva were Raymond H. Paynter, Jr., ornithologist and leader of the party, Robert T. Paine, 3rd, assistant ornithologist, Elisha F. Lee, mammalogist, Robert L. Dressler and Mrs. Ruth Oberg, botanists. Four natives assisted with the collecting and camp maintenance. Each member concentrated on his specialty but devoted some time to general collecting. The scientists' radius of activity was limited to the trail alongside the northern end of Lake Ocotal. After a month of intensive collecting (July 19–August 20) no one in the group had reached the opposite end of the 7-kilometer long lake or the pine-covered ridges along its southwestern side.

The scientific data on the plants and animals collected and observed in the immediate vicinity of Laguna Ocotal are presented in 9 independent reports. The first of these is a general introduction by Raymond A. Paynter, Jr. The vegetation about Laguna Ocotal is described in general terms by R. L. Dressler of the Gray Herbarium. A list of the Orchidaceae, by Mrs. Oberg, is said to be in press. The 39 species of Mollusca collected make up nearly one-half of the total known from Chiapas. J. C. Bequaert's report on the shells includes 9 species obtained by the expeditionaries outside the Selva and 49 species reported by others. Most of the ants from Laguna Ocotal were collected from epiphytes by the botanist Dressler. William L. Brown, Jr. identified 21 species, all of them widespread Neotropical forms. Four species of fish represented by 47 specimens were secured. Robert Rush Miller of the University of Michigan Museum of Zoology believes that 2 of the species might be new, but none of the specimens concerned were suitable for use as types. According to Benjamin Shreve, the 16 species of reptiles and 10 of amphibians collected include 3 first records for Mexico and five for Chiapas.

The 490 birds taken at Laguna Ocotal represent about 111 species. Eleven more species were seen. Nearly all the species are common, widespread forms, and the total represents about 20% of the entire Chiapas avifauna. Paynter, who reported on the birds, concluded that "the presence of pines at Laguna Ocotal, the one strikingly marked vegetational difference between the lowlands and the lake district, has almost no effect on the composition of the avifauna." The relationship of wing size and weight of bird to its flight performance is computed by Charles H. Blake from the weight data and wing outlines of 21 birds (19 species) supplied by Paynter. The mechanistic approach and the lone samples for each of 17 of the 19 species yield statistics of qualified value and contribute little of biological significance to the publication as a whole. Mammals collected by the leader of the expedition and Elisha F. Lee totaled about 117 specimens representing 16 common, widely distributed species. This may be less than 20% of a hypothetical total for the region. Two Harvard specialists, Francis L. Burnett and Charles P. Lyman, reported on this material.

None of the special collections from Ocotal stands up alone as worthy of a separately published report. The results of the studies confirm the long-held assumption that the fauna of the Selva Lacandona is the same as that of the better known and more readily accessible surrounding areas.

PHILIP HERSHKOVITZ

EVOLUTION

A REVIEW OF THE HABITAT OF THE EARLIEST VERTEBRATES. *Fieldiana: Geol., Vol. 11, No. 8.*

By Robert H. Denison. Chicago Natural History Museum, Chicago. $1.50 (paper). ii + pp. 359–457. 1956.

Whether the early vertebrates lived in fresh waters or in salt has long been a question of interest to paleontologists and physiologists. Homer Smith's work on kidney tubule structure and function, and the study of the oldest North American fossil vertebrates by myself and by Grove, have tended to swing opinion toward a belief in fresh-water origins. In the past few years, however, Robertson has presented an opposed opinion on the basis of hagfish physiology, and Gross has presented paleontological evidence favoring salt-water origins. The present paper is a further advocacy of the case for salt-water origins. The physiological evidence is but briefly treated. Denison's suggestion that the early marine vertebrates were functionally hypertonic to sea water and acquired a glomerular kidney tubule as a "preadaptation" to live in fresh water is far from convincing. On the other hand, his discussion of the paleontological data is a very able and well-reasoned one.

The evidence from the late Silurian and earliest Devonian is most important, since it is at this time that

we first find any considerable fauna of fishes. Interpretation of this evidence is, however, far from simple, as Denison notes. In many cases it is difficult to tell whether a given bed containing vertebrate remains is a marine or continental deposit; and further, it is certain a priori that in many cases the place where the remains came to rest is not the habitat of the animal in life. Denison considers in sequence the various Silurian and early Devonian collecting areas and then reviews the evidence for the various fish groups concerned. He concludes that at this time the Osteostraci and Anaspida were freshwater forms but that the early Heterostraci and Acanthodii were mainly marine, and that all vertebrates had earlier lived in the sea.

A. S. ROMER

CRITICAL NOTES ON EVOLUTION.

By William L. Fischer. William L. Fischer, München. $2.00 (paper). 111 pp. 1957.

The author states that "this paper is written by a layman for readers with open minds, with common sense and the ability to think by themselves." Its purpose is to point out the fallacies of Darwinian evolution, and to make a plea for the "special creation" hypothesis. Its interest to the biologist lies only in that it provides an excellent example of what a layman can do with scientific information which he does not understand, or is incapable of viewing objectively, in the effort to prove a particular point which he accepts in faith.

C. P. SWANSON

LEHRBUCH DER PALÄOZOOLOGIE. *Band I, Allgemeine Grundlagen.*

By Arno Hermann Müller. Gustav Fischer Verlag, Jena. DM 32.20. xii + 322 pp.; ill. 1957.

As the author notes in his preface, no comprehensive textbook in animal paleontology has been published in German for many years. The present volume, containing general and introductory matters, is the first of three planned to form such a text. The two further volumes are to be devoted to invertebrates and vertebrates; biostratigraphy is to be discussed in a separate future publication.

After brief introductory remarks and an equally brief history of the subject, approximately 100 pages are devoted to fossilization: the fate of the soft parts (and their occasional preservation); the vicissitudes often undergone by the skeleton before it is embedded, with particular attention to thanatocoenoses; and the changes, such as deformation and chemical modification or substitution, which may take place after burial. A brief but adequate explanation of taxonomy and nomenclatorial procedures is given.

Another 100 pages is devoted to phylogeny. Particularly because many readers of such a textbook will be students trained primarily in geology and with little biological background, one would have expected a broad introductory exposition of current evolutionary theory, followed by an application to the paleontological data. This is not the case; there are occasional scattered references to more general principles and theories, but they are mainly confined to topics discussed by Schindewolf and Simpson (mutation is defined (p. 189) as "das darwinistische Prinzip der 'zufälligen' und sprunghaften Änderung"). We are in the main treated to an account of the chronology of the geological development of various animal groups—an account which appears to have been taken, I expect, from a small book on this subject which the author published a short time ago (but which the reviewer has not seen).

A final major section of 50 pages treats of paleobiological problems, mainly from vertebrate examples, following much the pattern established by Abel in his ground-breaking *Paläobiologie* (not cited in the bibliography). An appendix on preparation is very sketchy; it is devoted mainly to microfossil preparation, and the author appears not to know the standard work on the subject by Camp and Hanna.

A. S. ROMER

EVOLUTION: THE AGES AND TOMORROW.

By G. Murray McKinley. The Ronald Press Company, New York. $4.00. x + 275 pp. 1956.

In this stimulating account of the evolution of the human mind, the author begins with the pre-living chemical situation in the early history of the earth. From simple inorganic compounds, complex organic molecules of various types were synthesized owing to the remarkable combining power of the carbon atom. The author traces steps from the evolution of amino acids to proteins and thence to a self-duplicating virus or "naked gene" level. There follows, in the first 4 chapters of the book, a sketch of our history from primitive bacterial cells to the stages of single-celled and multicellular organisms. The 5th chapter traces multicellular plant and animal progression in the course of evolution. The primary interest of the author is in the evolution and functioning of the human mind because, with the development of conceptual thought, man can begin consciously to help in the direction of his future.

Chapter 6 summarizes the interesting facts now available on the fossil history of the various types of early man, including Dart's man-apes of the Taung region of South Africa. Chapter 7 outlines the importance of social life and leadership in lower mammals and birds. The author also summarizes the development of complicated instincts in social insects such as termites, ants, and bees where there are no dominant individuals in the

society. Chapter 8, fascinating reading, describes the evolution of social life in early civilizations of man.

The first 8 chapters constitute approximately half of the book. The author devotes the next 4 chapters to the origin and development of the mental processes in lower animals and especially in man, and to the importance of conceptual thought in our evolutionary development. Chapter 11, on Instinct, describes von Frisch's experiments on communication in bees, and shows that these insects, operating solely by instinct, have actually developed a type of language.

The final chapters (13–17) will be the most interesting to non-zoological readers. Here the author uses past zoological facts to predict future history. He warns against the dangers of overpopulation not only in our own country but also in the world as a whole. Furthermore, he sees a real threat of declining intelligence in future human populations unless some sort of eugenic control is established. The last two chapters, Evolution and Ethics, and The Goal of Evolution, concern the broader implications of zoology. The author, a bold and thorough idealist, thinks that "science has arisen for no other reason than to make a choice amidst conflicting truths, or if none be found, to continue toward the final discovery of that which is real." He warns against the power of semantics, if wrongly used. He finds the chief contribution of our great religions to lie in teaching a good way of life. All great religious leaders have stressed "mutual aid" in their precepts. Mutual aid has a sound biological basis in gregarious animals lower than man. McKinley regards authoritarianism in religion as unscientific and unnecessary. He says, "Science is disciplined to guard itself against deifying tradition as truth. To insist that beliefs and morality should not be challenged by doubt is to imprison the race in eternal childhood." It seems to me that the recent interest among Christian ministers and religious leaders in this country in psychiatry may lead to an advance in religious thought.

I fully agree with the author as to the existence of a "basic drive toward companionship" which results in a desire to give aid to others, a basic human ethic. However, a "mutual aid survival ethic" is not necessarily the only alternative of a "tooth and claw" Darwinian competition. The author might also have considered the possibility of a "legitimate competition," not of the extreme "tooth and claw" variety. This "legitimate competition" is associated with the ethics of "good" sportsmanship. It seems to be a fundamental feature of man as a social animal, and would lead to a love of contests and development of leadership. The philosophy of such competition is discussed in Roy Bedichek's *Educational Competition*.

In several sections of this book the author expresses his belief that there is a "purpose" in the evolutionary goal, partly satisfied by the mind of man. Though using the word "purpose," the author denies a teleological argument. Yet to my mind, this repeated reference to "purpose" in evolution (excluding the conscious effort of man to control his own numbers and quality by eugenic methods), comes close to an assumption of the supernatural, in spite of the author's denial.

This book is highly recommended to all students of biology, philosophy, and religion. The author's style of writing is sincere and forceful. He is conscientious in giving credit to his references, and even includes a thumb-nail sketch of each book referred to in his bibliography. Everyone interested in present-day problems of our society should read *Evolution: The Ages and Tomorrow*, and every college library should have a copy.

SARAH B. PIPKIN

BIRD AND BUTTERFLY MYSTERIES. *The Truth about Migration.*

By Bernard Acworth; introduction by Brian Vesey Fitzgerald. Philosophical Library, New York. $7.50. 303 pp.; ill. 1956.

Two earlier books of the author have, in this instance, been bound together into a single volume, with the original text retained without great change. It deals essentially with bird and butterfly migrations, the cuckoo "mystery," patterns of mimicry and distribution of butterflies, and above all, with evolution. The author is an avowed anti-evolutionist, and except for his consideration of the laws of currents and of flight, which this reviewer can neither defend nor refute, the book is a plea for a return to the hypothesis of special creation by a "Personal, Living Designer." Evolution is considered to be a philosophical attitude rather than a scientific theory bolstered by fact—for example, no evolutionary information of recent years is discussed—so that little is to be gained by a dissection of the book and its theses other than to point out that the author, in his acceptance of special creation ideas and his rejection of Darwinism, is as guilty of blind prejudice as, in his mind, are those whom he belabors. The arguments pro and con are unlikely to impress either camp.

C. P. SWANSON

THE LIVING ROCKS. *Art and Nature Series.*

Photographed and devised by Stévan Célébonovic; Preface by André Maurois; Commentary by Geoffrey Grigson. The Philosophical Library, New York. $6.00. 85 pp.; ill. 1957.

The created beauties with which we surround ourselves, the art forms and color that please our eyes and stir our imagination and which we often think of as being solely the product of the artist, generally have their counterparts in nature. Indeed, it is to nature that the artist turns for inspiration when other sources dry up or stagnate. Primitive artists often admirably succeeded in blending art and nature, with the result that primi-

tive art itself has become a secondary source of artistic inspiration. In this beautifully illustrated volume, the artist-photographer, Stévan Célébonovic, has turned to rocks for his examples of beauty, and finds them in their crystal structure and in the fossils and fossil impressions. Particularly striking are his examples of limonite, manganese oxide on limestone and stibnite, and of a tertiary sea urchin, a cretaceous fish, a carboniferous fern-like plant, and a jurassic dragonfly. These are but a few of the 64 illustrations, all of them superbly done. An appreciative preface by André Maurois is followed by a commentary by Geoffrey Grigson which unites the illustrations into an organic whole. For those who might want to use the illustrations for evolutionary sequences, a geologic chart at the end will aid in correlating the illustrations with particular ages. This is an exceptionally fine piece of work, the first of a series with others to follow.

C. P. SWANSON

GENETICS AND CYTOLOGY

THE INHERITANCE OF COAT COLOR IN DOGS. *By Clarence C. Little. Comstock Publishing Associates, Ithaca.* $4.00. xiii + 194 pp.; ill. 1957.

The inheritance of coat colors of the various breeds of dogs can generally be understood by reference to the action of 10 different major genes. Various alleles of each locus are known, and it is apparent that modifiers, both genetic and non-genetic, contribute to the extent and intensity of pigment formation. Much of the genetic work was carried out by the author at the Jackson Memorial Laboratory at Bar Harbor, but breeders' records and previous literature were used to confirm and extend the author's findings. Breeders' records probably constitute a source of variable reliability, but Little has used these in a judicious manner in assessing their worth for genetic studies.

Following a description of his material and methods of collecting data, and a brief outline of genetic principles and of the process of melanin deposition, Little considers in detail the inheritance and action of each of the basic genes, and then analyzes 86 breeds individually for an expression of these genes. The breeds are grouped, according to the classification established by the American Kennel Club, into sporting dogs, working dogs, terriers, toys, and non-sporting dogs. The information is obviously more detailed for some breeds than for others, but the simplicity and clarity of presentation should make the book of considerable value to those who are in the business of breeding or who would like to know something of the inheritance of color in our most familiar domesticated animal.

C. P. SWANSON

MITOCHONDRIA AND OTHER CYTOPLASMIC INCLUSIONS. *Sympos. Soc. exp. Biol., No. X.* *Academic Press, New York.* $9.50. 198 pp. + 45 pl.; text ill. 1957.

The realization that regulated function is associated with regulated structure, and that an understanding of these relationships is amenable to experimental approaches, has led to a broadened attack on the structure of the cytoplasm and its component parts. The newer types of microscopes have been instrumental in permitting such studies to be made, and the result has been a much more intimate knowledge of the complexities of cellular architecture.

In the present volume, 3 of the papers deal with the Golgi apparatus. In a short article, Baker demolishes the ideas concerned with the reality of this supposed structure, and asks that the term be discarded as valueless. If the reader is inclined to agree with Baker's point of view, he will be surprised to find the same structure cheerfully resurrected by Lacy and Chalkie and by Dalton and Felix. The Golgi controversy remains, therefore, proponents and opponents ably marshal evidence to support their respective stands, and the biologist not immediately working on this problem cannot be other than confused.

Crawford, using neutral red vital staining for the most part, has studied the cytoplasmic inclusions in the snail amoebocyte, and contrasted them with what is found in chicken fibroblasts. His paper is largely descriptive, and few definite functions are to be associated with any inclusion except the mitochondria. Green deals with the cyclophorase system of enzymes and its structural relation to mitochondria; in particular, he discusses the enzymes of the fatty and citric acid cycles, the organization of the glycolytic system and its possible tie-in with protoplasmic membranes, the bound pyridine nucleotides, the particulate nature of the electron transport system, and the metallo-flavoproteins. The emerging thought is that structural unity of the enzyme systems enormously increases their efficiency as compared to similar systems of a non-particulate nature, and that structure and function are intimately related at the mitochondrial level. Duve and Novikoff, in separate papers, consider the enzyme heterogeneity of cellular fractions, and again, although the picture is somewhat blurred, the emerging pattern is that particular enzymes are associated with particular fractions, but that there is a heterogeneity of granules differing in enzyme content and activity.

Slater discusses the distribution of mitochondria (sarcosomes) in muscles. These granules are generally large in size, and are associated with the I and the A bands in cells which are concerned, respectively, with intermittent and sustained activity. They cannot be clearly separated from each other, however, although the A granules are larger and more numerous. On the

other hand, it does appear that these granules differ from those in liver cells in their enzymatic peculiarity.

Barer and Joseph present a provocative paper on a phase-contrast and interference microscope study of inclusions in living cells, and, in particular, on the relationship between mitochondria and the appearance and disappearance of the nuclear membrane. Their argument that much remains to be learned from intact cells is pertinent and timely. Randall, in another paper, deals with the fine structure of a protozoan, and more specifically, with the fibrous nature of the contractile elements. Chayen and Jackson present the only article dealing with plant tissues, and their study indicates the absence both of an endoplasmic reticulum and of any typical cristae mitochondriales. Their suggestion that the latter structures in animal mitochondria are homologous with the grana of plastids may or may not be taken seriously, but it is apparent from their work that plant mitochondria are not necessarily homologous—structurally or biochemically—with those in animals.

In general, the volume provides an excellent progress report of a most active field of biological research.

C. P. SWANSON

CHROMOSOMES. *Lectures held at the Conference on Chromosomes, Wageningen, April 16–19, 1956.*

N. V. Uitgevers-Maatschappij, Zwolle. Fl. 8.10. 231 pp.; ill. 1956.

This publication consists of 7 lectures given by the principal participants of this conference: E. Heitz; H. D. Springall; T. Caspersson; N. W. Pirie; L. Ehrenberg, A. Gustafsson, and D. von Wettstein; A. Müntzing; and C. D. Darlington. The first 4 papers are more chemically oriented. Heitz' paper, from the standpoint of a classically trained cytologist, considers chromosome structure, particularly heterochromatin, and calls for more investigation on the latter. Springall has presented an excellent summary of the physical and chemical methods by which the structures of nucleic acids and proteins are investigated, together with some description of recent advances in this field as they apply to the structure of nucleic acids and simple proteins. This article is especially recommended for background to the more classically trained cytologists. Caspersson has once more stressed the importance of quantitative data, particularly those obtained on nucleic acids and proteins by using the ultraviolet absorption method. Some advances in instrumentation were also included. The lecture of Pirie is also concerned with nucleic acid chemistry; in this case, however, the characterization of nucleic acids is by their chemical and physical behavior in a more general way. In Pirie's concluding remarks caution has been urged in the formulation of autocatalytic, self-copying duplication or reduplication mechanisms on the basis of present information.

The lecture of Ehrenberg, Gustafsson, and von Wettstein concerns a series of genetic studies carried out on plants of agricultural importance with a view toward eventual control of mutations. Müntzing has discussed the relation of chromosomes to the differentiation of plant species in plant breeding. In this respect polyploidy, both naturally occurring and experimentally induced, was considered the most important chromosomal event in the differentiation of new and agriculturally or ornamentally beneficial species. Darlington has presented a synthesis of ideas about the chemical and physical processes involved in cell division and genetic expression. As usual, in Darlington's writings, some of the theory is based on pure speculation, but it does present a challenge to the critical investigator and may stimulate new experiments.

As a whole, this book presents very little that is new to persons familiar with the work of the participants in the conference. It should, however, be useful to students in biochemistry, cytology, biophysics, or genetics who wish to see how matters stood in the various subspecialties of chromosome biology at the time of the conference.

R. R. COWDEN

THE PROCEEDINGS OF THE THIRD INTERNATIONAL CONFERENCE ON ELECTRON MICROSCOPY, LONDON, 1954.

Edited by R. Ross and a committee of 15. The Royal Microscopical Society, London. £4 10s. 0d. xvi + 705 pp. + 189 pl.; text ill. 1956.

ELECTRON MICROSCOPY. *Proceedings of the First European Conference, Stockholm 1956.*

Edited by F. S. Sjostrand and J. Rhodin. Academic Press, New York. $17.50. xi + 354 pp.; ill. 1957.

The size and diversity of these two volumes precludes any detailed analysis of their contents within the space of a short review. The Proceedings of the 1954 London symposium contains 158 separate papers, the 1956 Stockholm Proceedings 138 papers. The scope of the presentations ranges from physical theory, instrumentation, embedding, and sectioning to the submicroscopic elements of the cell, and from metallurgical applications to paper, textile, and chemistry studies. The papers concerned with any single topic are conveniently grouped in each volume, and while each paper is generally only of abstract length, and consequently terse in structure, each is also reasonably complete with illustrations. Both volumes have had care exercised in their preparation, and the illustrations, with but few exceptions, are excellent in their clarity. Certainly these are volumes that the electron microscopist can ill afford to ignore, although it is equally evident that the

progress in this field is of such rapidity as to make them more in the nature of yearly progress reports.

C. P. SWANSON

CYTOLOGY AND CYTOCHEMISTRY OF MELANOMA CELLS. *Ann. N. Y. Acad. Sci., Vol. 67, Art. 4.*

By Sylvia S. Greenberg, M. J. Kopac, and Myron Gordon. The New York Academy of Sciences, New York. $2.00 (paper). Pp. 55–122; ill. 1956.

A detailed cytological and cytochemical study of spontaneous pigmented neoplasms that develop in platyfish swordtail hybrids is presented. There are 39 pertinent black-and-white photomicrographs. The authors investigate the mode of action of the genetic factors involved in the atypical pigment cell growth and report in meticulous detail.

ROBERT G. CHAMBERS

BIOCHEMICAL CYTOLOGY.

By Jean Brachet. Academic Press, New York. $8.80. xi + 516 pp.; ill. 1957.

During the last ten years cytochemistry has become a legitimate subspeciality in biology, attracting workers with a variety of formal backgrounds: classical cytologists, experimental embryologists, biochemists, physical chemists, bacteriologists, and others. Most of these people have focused their attention on problems relating to nucleic acid and protein synthesis; in short, on problems of growth and differentiation within their specific spheres of interest. This book, however, is the first real effort to bring together this information within a conceptual framework. By great good fortune this difficult task has been attempted by a worker whose thinking and experiments have been a major impetus within the field. The resulting volume is a synthesis of the results of investigations in which the tools and techniques of the various subspecialties of modern biology have been applied. Each section starts with a morphological consideration of a particular cell organelle or constituent and proceeds to a description of its fine structure as demonstrated by the instrumental methods of electron microscopy or light microscopy. Cytochemical information derived from specific staining methods and autoradiographic studies follows. These are subsequently related to biochemical work on the same system. This unified treatment has been given to a full range of organisms, from virus to vertebrate. In order, the chapters consider: the cytoplasm of the resting cell, the nucleus of the resting cell, mitosis, nucleic acids and protein synthesis, nucleocytoplasmic interactions in unicellular organisms, the nucleus and cytoplasm in embryonic differentiation, and cancer cells.

This book has been written for those workers in any of the mentioned subspecialties of biology connected with growth and differentiation; it is not a general treatise of cellular physiology. It has the virtue of having been written by a biologist for biologists rather than by a biochemist for biochemists. Thus the chemical detail, in terms of structural formulae, reaction mechanisms, etc., has been kept to a level which should be understandable to a biologist without an extensive chemical background. Yet it has still been kept in a form which should not be offensive to the biochemist.

In addition to its organization, many fine illustrations, and excellent references, the work is a source of ideas, drawing together the results of the investigations of the past two decades and pointing to promising directions for new research. As such, it should be almost indispensable to experienced investigators and students alike.

RONALD R. COWDEN

BASIC MECHANISMS IN RADIOBIOLOGY. *IV: Cellular Aspects. Proceedings of an Informal Conference, Bear Mountain, New York, May 12–14, 1955. Nuclear Science Series, Report No. 18.*

Edited by Harvey M. Patt and E. L. Powers. National Academy of Sciences—National Research Council, Washington. $1.50 (paper). ix + 190 pp.; ill. 1956.

Cell biologists will find the candid discussions in this timely volume enjoyable and stimulating reading. Competently led by Zirkle, Tobias, Swanson, Spiegelman, and Mazia, the 5 discussions focus attention on information obtained by radiobiological methods in the study of cell division, on mitosis, and to a lesser extent, on mutation and chromosome breakage. Sprightly comments and queries, freely interspersed in the text of each paper, extend the scope of discussion and at the same time point out in striking fashion gaps in our knowledge and understanding of these fundamental biological processes.

PHILIP E. HARTMAN

GENERAL AND SYSTEMATIC BOTANY

PLANTS OF THE BIBLE.

By A. W. Anderson. Philosophical Library, New York. $6.00. 72 pp. + 12 pl. 1957.

During the past three hundred years, innumerable attempts have been made to identify the many plants mentioned in the Bible. As the interest in the subject is a very hardy perennial, and as the chances for a correct identification of many of these plants are practically zero, we may expect these attempts to continue indefinitely. New books on the subject should appear at fairly regular intervals. This particular book, however, differs markedly from the usual type of such works.

Here the emphasis is upon the 12 colored plates, reproduced from the 18th and 19th century books of Plenck, Duhamel, Redouté, Reichenbach, Hayne, Hornemann, Sweet, and of Sibthorpe and Smith. The original plates are beautiful and the reproductions are excellent. Indeed, the real value of the work lies in its illustrations, for the author describes a total of only 24 plants.

The treatment of each plant is brief and simple. First is printed the Biblical passage or passages that mention it. This is followed by a picture of the plant and a brief discussion, often less than a page, of the plant itself. The discussion often includes odd and interesting facts. The conclusions the author reaches are, very properly, tentative. The book as a whole is very pleasing, very nice to own, but why the author took the trouble to compose it is not clear.

CONWAY ZIRKLE

PLANT PHYSIOLOGY

ANNUAL REVIEW OF PLANT PHYSIOLOGY, *Vol. 8. Edited by A. S. Crafts, Leonard Machlis, and John G. Torrey. Annual Reviews, Palo Alto.* $7.00. 477 pp. + 1 pl.; text ill. 1957.

The previous volumes of this series have been widely accepted by plant physiologists and other plant science workers. The present volume maintains the high standards set in the earlier ones. Several innovations are to be found. There is a prefatory chapter by W. J. V. Osterhout summarizing work carried out on aquatic plants in the author's laboratory. Osterhout was one of the early workers to recognize the value of certain aquatic plants in studying fundamental problems of permeability and salt accumulation. The chapter not only gives a historical survey of the field but points out where aquatic plants may be useful in future investigations.

The second new feature is the inclusion of a chapter devoted to the physiology of a single plant—in this instance, sugarcane. This review was prepared by G. O. Burr and coworkers at the Hawaiian Sugar Planters' Association. Sugarcane is grown in most of the tropical parts of the world and an extensive literature about it has grown up. Much of this literature is not available in English or in journals commonly available to plant science workers.

The review on The History and Physiological Action of the Gibberellins, by Bruce B. Stowe and Toshio Yamaki, is most timely in view of the widespread current interest in these compounds. The gibberellins have been an object of research by Japanese botanists for approximately thirty years. This chapter summarizes the gibberellin work emphasizing the Japanese contributions.

It is not possible to discuss all the other reviews; they will simply be listed. Apparent Free Space (G. E. Briggs and R. N. Robertson); Mineral Nutrition of Plants (H. G. Gauch); Nitrogen Metabolism in Plants; Ten Years in Retrospect (F. C. Steward and J. K. Pollard); Photochemistry of Chlorophyll (J. L. Rosenberg); Biochemistry of Chloroplasts in Relation to the Hill Reaction (K. A. Clendenning); Auxin Relations in Roots (B. Aberg); Stock and Scion Relations (W. S. Rogers and A. B. Beakbane); Ascent of Sap (K. N. H. Greenidge); Drought Resistance in Plants and Physiological Processes (W. S. Iljin); Mass Culture of Algae (H. Tamiya); Permeability of Plant Cells (R. Collander); Physiology of Phloem (K. Esau, H. B. Currier, and V. I. Cheadle); Physiological Ecology (W. D. Billings); Physiological Genetics (H. J. Teas); Effects of Antibiotics on Plants (P. W. Brian); and Soluble Oxidases and Their Functions (W. D. Bonner, Jr.).

G. R. NOGGLE

PHOTOSYNTHESIS *and Related Processes. Volume II, Part 2. Kinetics of Photosynthesis (continued); Addenda to Vols. I and II, Part I. By Eugene I. Rabinowitch. Interscience Publishers, New York.* $18.50. xviii + pp. 1211–2088; ill. 1956.

This is the third and last volume in the remarkable monograph on photosynthesis by Rabinowitch. The statistics concerning it are truly impressive. The work was begun in 1938 and was not finished until 1956. There are 1993 pages of text, and in the last book alone there are approximately 1000 references. It is quite obvious that all of the references have been read, digested, and integrated into the larger picture, and a great many of them have been read very critically. It seems unlikely that anyone else could have accomplished a job as enormous as this, and have managed to stay interested and interesting to the very end.

The present book finishes the material on the kinetics of photosynthesis: rates as affected by pigment concentration and temperature, induction phenomena, and flashing light experiments. In addition it contains 500 pages of "addenda"—new material, relevant to chapters already completed and published in the two earlier volumes. Notable among the addenda are the very large advances in knowledge of the chemical path of carbon dioxide fixation, and a number of extremely beautiful electron micrographs of chloroplasts and chloroplast sections.

Not only are there these 500 pages of Addenda and Miscellaneous Additions. Even in the Preface the author records, with regret, a few more highly significant experiments that were published just a little too late to be treated fully in the text. This race to include all of the last-minute material could only have

been expected in a monograph attempting such a frighteningly complete review of a rapidly expanding, experimental area.

It may never be possible to assess fully the effect of this series on the rate of progress in the field of photosynthesis. By providing a complete orientation for anyone not initiated, it undoubtedly permits freer and easier entry into the field. It probably has enabled some workers to avoid a duplication of experiments. At the very least, it is an enormous time-saver for anyone faced with the job of compiling bibliographies on photosynthesis. Above all, it is an outstanding monument of massive scholarship in a scientific field.

A. T. JAGENDORF

ENCYCLOPEDIA OF PLANT PHYSIOLOGY. *Vol. VII: The Metabolism of Fats and Related Compounds.*

Edited by W. Ruhland; M. Steiner, subeditor. Springer-Verlag, Berlin, Göttingen, and Heidelberg. DM 108. x + 512 pp.; ill. 1957.

This book is Volume 7 of a projected 18-volume *Handbuch der Pflanzenphysiologie—Encyclopedia of Plant Physiology*. The entire work is under the general editorship of H. Ruhland with the assistance of co-editors from England, the United States, and Europe. The present volume was edited by H. Steiner of the University of Bonn and contains 13 chapters prepared by workers from Germany, France, the United States, and Great Britain. Nine of the chapters are in German, 3 in English, and 1 in French.

With the exception of some recent work on the biochemistry of fat formation, plant physiologists in the United States have not worked extensively on the vegetable fats. Perhaps this is due to the fact that we have had an ample supply of animal fats, and no economic pressure was felt to explore new fat sources. In Great Britain and Europe, however, animal fats have been in short supply and a great deal of work has been done on vegetable fats. This volume brings together the scattered literature on this subject and provides a very valuable reference work.

The volume is organized under the following general headings: The Plant Fats (higher plants, algae, fungi, bacteria), The Enzymes of Fat Metabolism, The Biochemistry of Fat Formation, The Physiology of Fat Synthesis and Fat Storage, The Mobilization of Fats during Germination, The Agriculture Significance of Plant Fats, and The Phosphatids and Glycolipids. Each chapter provides a critical survey of some aspect of fat metabolism and is amply documented. A German-English, English-German subject index is provided, as well as an author index.

G. R. NOGGLE

ECONOMIC BOTANY

FUNDAMENTALS OF HORTICULTURE. *Second Edition.*

By J. B. Edmond, A. M. Musser, and F. S. Andrews. McGraw-Hill Book Company, New York, Toronto, and London. $6.75. xiii + 456 pp.; ill. 1957.

In this second edition, as in the first, the emphasis is chiefly on the fundamentals of plant growth and their application to production problems. To make this feature more valuable, the practices and statistical material have been brought up to date; changes have been made in the sets of questions at the end of each chapter to make them more applicable to present-day problems; the section on citrus fruits has been revised; and information regarding the use of plant regulators in apple orchards has been added.

Otherwise the book is but little changed. In Part I (6 chapters) the fundamental plant processes, tissues and structures, are discussed. Part II (9 chapters) treats of the principal horticultural practices; while Part III (9 chapters) deals briefly, but adequately, with the more important horticultural crops, fruits, vegetables, and ornamentals. The value of the book might have been enhanced if the genus and species had been indicated in each case.

ALBERT F. HILL

LABORATORY EXERCISES IN HORTICULTURE. *Third edition, revised.*

By Harry E. Nichols and Ernest S. Haber. Iowa State College Press, Ames. $2.25 (paper). 121 pp.; ill. 1957.

This laboratory manual, now in its third edition, may be used in connection with any course in general horticulture, since all the important aspects of this science are included. Each of the 20 exercises follows the same general pattern. A preliminary discussion furnishes the necessary background. Following this, the objectives, methods, and procedure are usually listed, together with specific problems. A new subject, Lawns—Planting and Care, has been added in this edition. The exercises on fruit and vegetable production have been brought up to date, many new varieties included, and suggestions for outside reading have also been increased. Much of the material is organized in tables, and the manual is well illustrated with sketches and photographs.

ALBERT F. HILL

DECIDUOUS ORCHARDS. *Third edition, revised.*

By William Henry Chandler. Lea & Febiger, Philadelphia. $7.50. 492 pp.; ill. 1957.

The original purpose of this book was to give the reader

a comprehensive survey of the most dependable information available regarding deciduous fruit trees. In this second revision much new material has been incorporated, such as the use of plant hormones and hormone-like regulators. Often the actual experiments that supplied the evidence are described. Of necessity, however, no attempt has been made to make an exhaustive review of the recent literature. Only a sampling is included, choosing reports that most readily fit into the text.

Part I (7 chapters) is devoted to a discussion of the tree, its flower and fruit. The 5 chapters which constitute Part II treat of the environmental factors; the 3 chapters in Part III deal with the growing and training of deciduous orchard trees. Individual species are discussed in considerable detail in Part IV. Its 6 chapters are devoted to pome fruits; stone fruits; the mulberry and fig; the persimmon, northern papaw, pomegranate, and jujube; edible nut trees; and the tung oil tree.

A bibliography with 527 titles presents a representative selection of recent papers reporting the results of research on fruit trees.

ALBERT F. HILL

GENERAL AND SYSTEMATIC ZOOLOGY

GENERAL ZOOLOGY.

By David F. Miller and James G. Haub. Henry Holt & Company, New York. $6.50. viii + 550 pp.; ill. 1956.

The authors have produced a better than average textbook to introduce general zoology to reluctant readers. Their terse, choppy style may slow down versatile readers, but in this manner the authors succeed in using a limited vocabulary to present the material clearly and still cite an adequate number of examples to explain the subject matter. On occasion, the authors devote too much space to irrelevant examples, although these are usually interesting discussions. The text is well illustrated with photographs and simple drawings, although occasional composite illustrations could be used.

Nearly half of the text is devoted to a systematic discussion of the types of animals. There is a lengthy discussion of the economic importance of many groups. In the higher invertebrates more space is accorded the variety of forms within each phylum than is given to basic morphology. Two short sections, one on genetics and one on evolution, which follow the presentation of the animal groups, are excellent explanations of the material in the previous section, and add meaning to the lengthy treatment of the animal groups. The latter third of the text is devoted to a discussion of the animal organ-systems and their functions. The content is presented in a manner which allows this section to be used as a beginning section in many courses, but the coverage will not be complete enough in detail for many introductory courses. This textbook should receive serious consideration by those who are selecting a text for a one-semester course for non-zoology majors.

DONALD W. TWOHY

GENERAL ZOOLOGY. *Third Edition.*

By Tracy I. Storer and Robert L. Usinger. McGraw-Hill Book Co., New York, Toronto, and London. $7.50. vi + 664 pp.; ill. 1957.

This popular text (2nd ed., *Q.R.B.*, 28: 73. 1953) has undergone extensive revision with respect to the introduction of new material, printing style, and illustrations. The fundamental aspects of dynamic biology, e.g., genetics, physiology, and cytology, have received an enlarged and somewhat more detailed treatment which should increase the background of beginning students for subsequent courses in zoology. The treatment of the phyla of the animal kingdom, which composes the second part of the book, is excellent. This revision of what many zoologists have considered the finest introductory zoology textbook available has resulted in an even better, modernized text.

RONALD R. COWDEN

ATLAS DES LARVES D'INSECTES DE FRANCE, *Vers Blancs, Chenilles, Asticots. Nouvel Atlas d'Entomologie, Number 10.*

By Renaud Paulian. Editions N. Boubée & Cie., Paris. 1,800 fr. (paper). 222 pp. + 22 pl. (4 in color); text ill. 1956.

Illustrated by many text figures and 20 plates, of which 16 are of line drawings and 4 (of Lepidoptera) are in color, this small book describes and characterizes examples of the immature stages of nearly all of the chief groups of insects of France. Simple keys are given to the orders and, in the larger orders, to the chief families. Most of the families and even many of the genera, Holarctic in distribution, also occur in North America. Considerable general information is given about the life histories and larval habitats of many of the groups.

ALEXANDER B. KLOTS

AQUATIC INSECTS OF CALIFORNIA, *with Keys to North American Genera and California Species.*

Edited by Robert L. Usinger; 16 contributors. University of California Press, Berkeley and Los Angeles. $10.00. x + 508 pp.; ill. 1956.

This is a book for everyone interested in aquatic insects or in the general study of limnology, even though it deals specifically with insects found only in California. Aquatic communities the world over have, as Usinger points out, the same major groups of species: "Thus a stream in South Africa may resemble a stream in California . . . a pond in Sumatra and a lake in Sweden will resemble, in a general way, comparable bodies of water in North America."

The beginning student in limnology will find valuable and concise discussions of the role of insects in an aquatic community and their special adaptations to it; a classification and description of aquatic habitats which, although related specifically to California, can be applied, for the most part, anywhere; and useful sections on mosquito and gnat control, reservoirs and irrigation, water pollution, pond fish culture and stream and lake management. These sections, as well as the chapter on equipment and technique, bear the stamp of practical experience.

The thirteen orders of insects which are wholly or partially aquatic are each treated separately, but in a uniform manner, by a specialist in the group. A general characterization of the order is followed by a pertinent discussion of its role in the aquatic community or specialized habitat, and by collecting and preparation techniques. Keys to the California families, genera, and species of each order, with special notes on individual groups, are of widespread use, since the majority of the genera and many of the species are far more extensive in their distribution. Each chapter is exceedingly well illustrated, and although most of the illustrations have been borrowed from other publications, their authenticity and aptness make them valuable additions. Each chapter also has its own bibliography. A glossary of terms at the end of the book supplements the brief preliminary chapter on insect structure.

Although this is primarily a compilation, the material is well selected and unified. Usinger and his 15 cooperating authors have done us all a great service.

ELSIE B. KLOTS

EVOLUTION AND CLASSIFICATION OF THE MOUNTAIN CADDISFLIES.

By Herbert H. Ross. The University of Illinois Press, Urbana. $6.00. viii + 213 pp.; ill. 1956.

Some 5000 species and thirty families of Trichoptera have up to now been described. Although the fossil record of their evolution is far from complete, we do know that recognizable caddisflies existed in the Upper Triassic and that by the mid-Tertiary they had evolved well along the paths which they were to follow to the present day. With the publication of this volume we have a convincing picture of the phylogenetic development of these families (based on wing venation), as evidenced by fossils; on morphological characters of larvae, pupae, and adults; on larval behavior and case-making habits; and on statistics of dispersal, both recent and fossil. A plethora of charts describing the phylogenetic dispersal, recent distributions, and phylogenies of species, genera, and families, as well as hundreds of drawings of genitalia, punctuate the author's evaluations of previously held views and his own well-documented opinions.

The three most primitive families: the retreat-making Philopomatidae, the case-making Rhyacophilidae, and the Glossosomatidae, have been studied in detail. They are made up, for the most part, of "cool-adapted" species that afford excellent opportunities for comparative studies since, being restricted to swift as well as to cool waters, they are limited to hilly or mountainous regions; since related groups occur in mountains the world over even though widely separated; and since they represent survivals of a great number of phyletic lines.

In addition to the detailed account of the evolution and dispersal of each of these 3 families, there is a synoptic account which includes keys to subfamilies, genera, and species; designation of type species; reference to the original description of each species; and descriptions of 4 new genera, 7 new subgenera, and 37 new species.

This is an inspiring and scholarly piece of work which sets high standards for anyone working within the order. It will also prove of great interest to many biologists not interested specifically in caddisflies or even in insects, exemplifying, as it does, thorough, yet highly speculative, phylogenetic work.

ELSIE B. KLOTS

A MONOGRAPH OF THE ITHOMIIDAE (LEPIDOPTERA), *Part 1. Bull. Amer. Mus. nat. Hist., Vol. 111, Art. 1. By Richard M. Fox. American Museum of Natural History, New York.* $1.50 (paper). 76 pp. + 9 pl.; text ill. 1956.

This, the first part of the author's projected revision of the Neotropical butterfly family Ithomiidae, covers the subfamily Tellervinae, with 1 genus, and the tribe Tithoreini of the subfamily Ithomiinae, containing 8 genera. The very extensive remainder of the family, composed of the other 7 tribes of the Ithomiinae, will be covered in subsequent publication. Figures of the palpi, legs, venation, and male genitalia—the chief taxonomic characters used—are given for most of the species. Photographs, not very well reproduced, show the patterns of the species and subspecies. Outline maps (uncomfortably small) are used to show the distribution patterns of the species and subspecies. Full (and excellent) bibliographic references are given.

The distributional data and full counts of all specimens studied are given in detail. In all, 20 species, 1 of which is new, and 42 additional subspecies, 7 of which are new, are recognized.

The chief general interest and value of this excellent work stems from two facts. Firstly, the Ithomiidae is one of the two chief families of butterflies, the Heliconiidae being the other, that are concerned in the famous riot of Müllerian mimicry that characterizes the Lepidoptera of the Neotropical Region. We shall never have a really sound basis for many important conclusions about this mimicry, so much discussed and argued about, until really sound taxonomic studies such as this have been made of all of the groups concerned. Secondly, most previous taxonomic work on the group has been so strongly influenced by the undue importance attached to superficial characteristics that a revision based on really significant ones, and on adequate material, as this one is, is bound to clear up many misconceptions. In this respect the author's detailed discussions of his nomenclatorial and systematic procedures are very worthwhile. So are his phylogenetic conclusions and his reasons for considering the Ithomiidae a separate family at a time when serious discussions of this matter are developing, and some authorities are tending to lump this group with the Danaidae, Nymphalidae, Heliconiidae, Satyridae, and Acraeidae into a single family.

ALEXANDER B. KLOTS

A REVISION OF THE GENUS *TRIDREPANA* SWINHOE (LEPIDOPTERA: DREPANIDAE). *Bull. Brit. Mus. (nat. Hist.), Ent., Vol. 4, No. 9.*

By Allan Watson. British Museum (Natural History), London. 30s. (paper). Pp. 407–500 + 2 pl.; text ill. 1957.

As a systematic revision of a restricted genus of moths of the Indo-Australian region, this is in most ways a model of what such papers should be. In nearly all instances adequate material was obtained for study by borrowing widely from other museums. The types of virtually all of the names were studied. Both male and female genitalia were studied and figured whenever possible. The full data available for all specimens were listed. Photographs are given of those species not previously illustrated elsewhere. Eleven species out of a total of 34, and 11 out of a total of 15 additional subspecies, are described as new. Some interesting discussions of geographic subspeciation are given. We note with interest the demonstration of structural differences between some subspecies, in view of the claim made by some workers that any structural difference is an indication of at least specific difference. In some instances we note that the author has described new subspecies based on what can hardly be regarded as adequate material, e.g., the subspecies *unita* of *T. flava* (Moore), and the subspecies *brevilinea* of *T. argentistriga* (Warren), each described from two male specimens only. Such new names may be "good," but more material than that will be needed to prove it.

ALEXANDER B. KLOTS

A REVISION OF THE AUSTRALIAN CHAFERS (*Coleoptera: Scarabaeidae: Melolonthinae*). *Vol. I.*

By E. B. Britton. The British Museum (Natural History), London. £4. viii + 185 pp. + 42 pl.; text ill. 1957.

Most of the beetles of countries far away from the centers of entomological activity during the 19th century were described in scattered publications, and it is almost impossible for anyone but a specialist to get a comprehensive view of a particular group. Even he encounters difficulties. It is therefore gratifying when a monograph such as the present one appears. It deals with 5 of the 13 tribes into which the author divides the subfamily Melolonthinae of the Scarabaeidae (Sericini, Xylonchini, Phyllotocidiini, Automolini, Macchidiini). The work was based on a study of the types of most of the species and a large collection of specimens available to the author. The monograph describes 203 species, 67 of these new. There are the usual keys to the genera and species, detailed descriptions, and other information for each species. The types are clearly identified. Twenty-five drawings of the entire insects accompany the text, as well as numerous drawings of anatomical details, including those of the male genitalia.

It appears that the Australian Melolonthinae are remarkably isolated. Most of the Australian genera occur nowhere else. The habits seem to be similar to those of the American and European Melolonthinae. Many species are of economic importance because the larvae feed on the roots of many plants, while the adults feed on the leaves of shade trees, and damage vines and orchards.

G. H. DIEKE

A MONOGRAPH OF THE IMMATURE STAGES OF AFRICAN TIMBER BEETLES (CERAMBYCIDAE).

By E. A. J. Duffy. The British Museum (Natural History), London. £5 5s. vii + 338 pp. + 10 pl.; text ill. 1957.

This is the second volume of a series of monographs on immature stages of timber beetles. The first, on British species, appeared earlier (1953), served as a model for the present volume, and treated also more general matters. The third volume (South and Central America, West Indies) is in preparation.

Keys are given to the larvae and pupae of 203 and 83 species, respectively, and include all those of major economic importance. Beautifully executed figures of details of larvae and pupae accompany the text, as well as figures of many adult forms. The plates contain mainly photographs of damage caused by the larvae. All available knowledge on the biology of these beetles is given either from original observations or from previously published data. An extensive list of references is added.

While the number of species treated is of course only a small part of those existing in Africa, the monograph represents such a tremendous step in advance over what was previously available that it will form the foundation on which all further work on the immature stages will have to be based.

G. H. DIEKE

A MONOGRAPH ON THE TERMITOPHILOUS STAPHYLINIDAE (*Coleoptera*). *Fieldiana: Zool., Vol. 40. By Charles H. Seevers. Chicago Natural History Museum, Chicago.* $6.50 (paper). 334 pp.; ill. 1957.

This monograph is of more than usual interest. It does not deal with a particular taxonomic unit, such as a tribe or subfamily, but with an ecologically connected group, namely, all those beetles of the family Staphylinidae which live in the nests of termites. The author excludes those species found only accidentally with termites or merely predatory on them. Most of the nearly 300 species treated in the monograph belong to the large and taxonomically very poorly known subfamily Aleocharinae.

A systematic revision of the various groups containing termitophilous staphylinids is given, with a description of many new species. Particular emphasis is placed on the biological relationships between the termites and their guests, a relation which required a review of the systematics and biology of the termites themselves. The author stresses particularly the phylogenetic implications of his work and attempts to reconstruct the evolution and migration of the species in past geological eras.

Termitophilous beetles are found practically everywhere termites exist, which is principally in the tropical parts of the world. A few species reach temperate zones. These beetles are particularly well represented on the American continent, 16 species being known from the United States.

G. H. DIEKE

VERTEBRATES OF THE UNITED STATES. *By W. Frank Blair, Albert P. Blair, Pierce Brodkorb, Fred R. Cagle, and George A. Moore. McGraw-Hill Book Co., New York, Toronto, London.* $12.00. ix + 819 pp.; ill. 1957.

Since Pratt's *Manual of the Vertebrate Animals of the United States* became unavailable some ten years ago, there has been no general reference for the identification of vertebrates of the United States. The authors of this book have very ably filled this gap, and once again in a single volume are to be found keys for all the vertebrate groups. It is an added advantage that the classification is current, and the scientific names of the various taxa are those presently in use.

The book is really five units within one cover, for each of the major vertebrate groups is treated separately. Each part begins with a brief outline of the geologic history of the group and the relationships of the higher categories within the class. For most groups the introduction also contains a discussion of some of the anatomical structures peculiar to the group.

The style of each section is the same except that in the fishes two classes, rather than only one, are treated. Under each class there are dichotomous keys to the orders. After characterization of the order there follows a key to the families within it. Each family is treated in turn, being characterized in telegraphic style, closing with a statement of the geologic period in which the group appeared. This is followed by keys to the genera, and under each genus there is a key to its species. Finally, each species is briefly described and its geographic distribution stated. Families with only one genus, and monotypic genera, lack keys, but all categories with two or more forms in them receive the full treatment.

The keys themselves are well-constructed and simple to use. Yet one must object to the use of key choices that are based solely on geographic distribution, as distribution is not in itself taxonomic. It is difficult to visualize how being restricted to the vicinity of Mount Shasta can be of taxonomic importance as compared to not being so restricted, or how, in the apparent absence of structural features, distribution east or west of the 100th meridian can be of taxonomic significance. Only in the sections on reptiles and birds has the use of geographic distribution as a key character been completely avoided.

In the section on birds there is an extensive discussion of the structures that are used in separating the higher categories, and there are descriptions and diagrams of the various types of palate, leg tendon, leg musculature, and intestinal looping that are used to diagnose the various orders of birds. The section is definitely not a field guide to birds, but uses sound taxonomic characters throughout.

The book is profusely illustrated both with line drawings and selected photographs. All are of high quality and clarity. Not a few are originals produced by the authors. Both authors and publisher are to be

commended for the quality of the book, which doubtless will be a standard reference for many years to come.

BRYAN P. GLASS

A STUDY OF THE SHARKS OF THE SUBORDER SQUALOIDEA. *Bull. Mus. comp. Zool. Harv., Vol. 117, No. 1.*

By Henry B. Bigelow and William C. Schroeder. Museum of Comparative Zoology, Cambridge. $2.25 (paper). 150 pp. + 4 plates; ill. 1957.

This incredible team of ichthyologists has zealously tackled the study of another group of elasmobranchs in their concerted effort to make order out of chaos in an ill-defined group of chlordates. Some of these unconventional-looking sharks without anal fins, including, among others, the spiny dogfishes and bramble sharks, are familiar to many biologists. Recognizing that lack of material and complex taxonomic questions have impeded their work, they remark, "We attempt little more in the following pages than to summarize the present state of knowledge of the group. Anything as ambitious as would be implied by the word 'revision' is a task for the future."

Seventeen genera are reviewed in some detail along with diagnostic keys for discriminating between the two families in the suborder and all the genera. For some unexplained reason, dichotomous keys are given for the separation of only about one-half of the species among all the genera. A great deal of information on the Squaloidea of the Western North Atlantic has already been published in the monograph of the sharks of that region, where, interestingly enough, the same authors cited over 350 literature references in the synonymy of the spiny dogfish, *Squalus acanthias*. Virtually nothing has been published on some of the other forms covered in the present study.

As with many systematic reviews dealing with large, rare, or difficult-to-procure species, this study suffers from a lack of detail in regard to individual, ontogenetic, and geographic variation. Stated differences between genera and species in diagnostic keys based on small samples and a lack of critical data on variation create knotty problems in the accurate identification of sharks, a situation to which the reviewer can attest from using their keys. This loss can be corrected in the future if students who have an opportunity to identify sharks and rays can measure as many individuals as possible in a wide range of sizes according to standards set up by these authors. Particular effort should be made to take measurements of body proportions that can be expressed as the regression of one dimension on another, such as the regression of head length on the total length, rather than as ratios. The necessity for the comparison of regressions rather than ratios arises from the fact that in sharks different parts of the body grow at different rates.

These authors established a unique, critical treatment and original outlook on elasmobranchs in their other monumental studies. In that same tradition, this paper is a solid, bold, and well-organized contribution, based on a critical examination of fresh and preserved specimens, the latter from all over the world. A large part of the text consists of a careful appraisal of the polyglot literature listed in 15 pages of references. It is superbly illustrated with line drawings by E. N. Fischer, J. H. Sawyer, and the senior author. There is no doubt that this study will serve as a required reference for all students of sharks for many years to come.

ROMEO MANSUETI

THE AMPHIBIA OF CEYLON.

By P. Kirtisinghe. Published by the Author, Colombo. $3.00. xiii + 112 pp. + 1 pl.; text ill. 1957.

The Ceylonese amphibians, according to this excellent summary of Kirtisinghe, consist of 5 species of toads, 12 true frogs, 8 racophorids, 8 microhylids, and 2 caecilians. There are no salamanders. The fauna is similar to that of southern India; however, there has been active speciation since the end of the Pleistocene, as the 14 species of anurans that are found solely in Ceylon indicate.

The book is supplied with identification keys and there are good drawings of the adults and, where pertinent, the tadpoles. Each species account includes a synonymy, a fairly detailed description, habitat and habit information, description of the tadpole, and distribution. There is a literature list of about 120 items, and an index to specific and subspecific names. A map showing some of the important physical features of the island would have been a welcome addition. The little volume begins with a colored frontispiece and a charmingly written introduction which contains a brief history of our knowledge of the amphibia of Ceylon.

ARNOLD B. GROBMAN

REPTILES.

By Angus d'A. Bellairs. Rinehart & Company, New York; Hutchinson's University Library, London. $1.50. 195 pp.; ill. 1957.

This is an excellent little book for a biologist who wishes to learn some fundamental and interesting facts about reptiles. It is too sophisticated for laymen, and it is not an illustrated guide to species. Its concern is with the broad biology of reptiles, living and extinct, especially their evolution, morphology, physiology, and

life-histories. After some 60 pages of general introductory material, the remainder of the book discusses the various major groups of reptiles. This is the type of presentation, of a body of biological knowledge, in which British authors often excel. The book is authoritative, interesting, compact, and inexpensive.

Occasionally its compactness gives rise to misleading impressions, as, for example, where Bellairs says that the eggs of reptiles are laid on land (p. 10). While this is true for eggs that are deposited somewhere, it clearly does not include those instances in which the eggs are retained within the oviducts and the young are born alive. The point is eventually clarified, as the author gives an excellent brief review of viviparity in reptiles in his last chapter.

One might wish for just a little less saving of space. For example, the same set of legends is used for a series of figures occurring on different pages, and the bibliography of papers and articles does not include titles. The general impression, however, is that this is a delightful book. Considering its price and the number of interesting facts and ideas it contains, it represents a genuine bargain.

ARNOLD GROBMAN

REVISION OF THE AFRICAN TORTOISES AND TURTLES OF THE SUBORDER CRYPTODIRA. *Bull. Mus. comp. Zool., Harv. Coll., Vol. 115, No. 6.*

By Arthur Loveridge and Ernest E. Williams. Museum of Comparative Zoology, Cambridge. $5.50 (paper). Pp. 163–557 + 18 pl.; text ill. 1957.

This comprehensive study of crypotodiran turtles, when taken in conjunction with a 1941 paper by Loveridge (dealing with the Pleurodira), comprises an up-to-date review of our knowledge of the turtles of Africa. Loveridge and Williams herein report on 33 species and subspecies, which are grouped into 17 genera and 4 families. Noteworthy is the use of subgenera, which are not often utilized in herpetological studies. Also commendatory is the consideration of extralimital forms where they shed light on the relationships of the African turtles. Available information on fossil cryptodires is incorporated into the species accounts.

Each species discussion typically includes the following topics: synonymy, common names (often in several languages), citations of illustrations in other works, location of types, morphological descriptions, color description, size, breeding, diet, longevity, parasites, habits, enemies, habitat, localities, and range.

The skulls and a few other morphological characters are illustrated with line drawings, and 14 plates show dorsal and ventral views. There are a number of outline maps showing localities, an index to the scientific names, and a bibliography of over 600 items. A footnote to the latter indicates that the Harvard group has an extensive bibliography of African herpetology in preparation for publication.

Some significant topics of broad interest are incorporated in the text. For example, there is a discussion of the relationships and groupings of the living trionychids (soft-shelled turtles), although only about a third of the known species are African. There are careful reviews of the testudinines and emydines with no temporal or geographic limitations. Future students, not realizing that the contents of this book are broader in coverage than its title indicates, might be unfortunate enough to miss some of its substantial contributions.

ARNOLD B. GROBMAN

HANDBOOK OF SNAKES *of the United States and Canada. Two volumes.*

By Albert Hazen Wright and Anna Allen Wright. Cornell University Press, Ithaca; [Comstock Publishing Associates, Ithaca.] $14.75. Vol. I: xviii + pp. 1–564 + 43 maps; ill. Vol. II: ix + pp. 565–1105 + 70 maps; ill. 1957.

This set of volumes joins a series of distinguished "handbooks" on American Natural History that includes titles on lizards, mammals, frogs and toads, turtles, aquatic plants, and spiders. These books on snakes contain a wealth of information. The 30-page introduction has much standard material and other matters not ordinarily included in similar works as, for example, the English equivalents of some Latin names; the identity of the person who first did a generic revision in snakes as a doctoral dissertation; maps of physical, geological, and vegetational features; and photographs of shed snake skins. The second volume ends with a glossary, a brief list of references, and an index of about 3000 items.

The bulk of the two books consists of accounts of the subspecies and species of snakes in the United States and Canada. The discussions are divided into sections corresponding to the families. Under each family, the accounts are arranged alphabetically by genus. Keys to families, genera, and races are included in appropriate places. A typical species account includes the following items: recommended common name and other common names, with an indication of how frequently the various names have appeared in the literature; scientific name and those synonyms that have been widely used; a series of photographs, usually of live specimens, showing several segments of the body and general dorsal and ventral views; a distribution map (which may include all the forms in a species group or genus;) geographic range; size range; distinctive characters (which are frequently quoted from recent revisionary studies); color (often original and based on a live snake in the Wrights' possession); habitat; period of activity;

breeding; food; field notes; and authorities. The authorities are listed only by name and date of publication, with an indication of the section of the bibliography in which the full citation occurs. Unfortunately, the third volume, which is to contain the bibliography, is not yet at hand at the time of writing this review.

The thing that most impresses one in reading these volumes is that they are stylistically so different from companion volumes by others, although similar to the book on frogs and toads by the Wrights. These are personalized natural histories. They contain long quotations from the Wrights' original field notes. One gets the impression that the Wrights have written a story about their own field adventures with snakes, that they have incorporated the information of others after long and diligent study, and that they have arranged the material in an orderly fashion. The result is not a cold, impersonal encyclopedia. A general theme running through the story is the warm recognition of the place of the field naturalist of the old school, who knew intimately his area with its plants and animals and its history. The Wrights do not discount the value of laboratory studies, but their sympathy with field observations is clearly evident.

Those who value crisp compendia of facts will find the volumes have frustrating features. Those who are humanistic natural historians will find the books replete with charming items. All, however, will find much substantial information of real interest.

ARNOLD B. GROBMAN

THE BIRDS OF ISLA COIBA, PANAMA. *Smithson. misc. Coll., Vol. 134, No. 9.*

By Alexander Wetmore. The Smithsonian Institution, Washington. $1.30 (paper). 105 pp. + 4 pl.; text ill. 1957.

Coiba is the largest island on the Pacific coast of Central America; it has a length of 21½ miles and a maximum width of 13 miles. The nearest point on the continent is the mainland of Panama some 15 miles away. This report on the birds will interest students of zoogeography, evolution, and animal behavior. Wetmore seems to be the first naturalist to spend a considerable period (a month) on Coiba, though others have paused there briefly—in 1901 a collection of birds was made for Lord Rothschild. The circumstance that Coiba has long served as the penal colony of Panama has discouraged visitors; it has also prevented the destruction of the lofty virgin forest that almost wholly covers the island.

Isolation from the mainland has enabled over 20 per cent of the resident bird species to diverge from their mainland relatives sufficiently to merit taxonomic status. Wetmore has named 16 new subspecies, in addition to 4 previously described from earlier collections. Some of these island races are so different in appearance that less than a generation ago they would have been deemed distinct species. In most cases the Coiba birds are characterized by intensification or darkening of color, probably correlated with greater rainfall on Coiba than on the mainland, at least in the dry season. Some birds show enlargement of the bill, an attribute of insular populations which is not unusual.

Perhaps more surprising than the evolution of insular races is the absence, from so large and well-forested an island, of many of the most characteristic neotropical families, genera, and species (e.g., tinamous, guans, toucans, motmots, trogons, etc.) which are found on the nearby mainland. Speculation is thus invited as to when Coiba became separated from the continent, how and when the local avian population originated, and what the ecological conditions and climate of the area were at that time. It is noteworthy that, with a few exceptions, all land birds of Coiba represent species that on the mainland are inhabitants of clearings, thickets at the edge of second-growth, or open woodland—areas of fairly low vegetation and abundant light. On Coiba, Wetmore found many of these species not only in the expected habitats, but also in the sunlit crowns of the tallest trees in the deep forest. On the mainland of Panama, the forest canopy is occupied by other species, absent from Coiba. Wetmore surmises that the ancestors of the resident birds of Coiba arrived after it became an island, for the species involved are all fairly strong fliers or such as might have been carried by storms. The geologic history of the area and of the nearby isthmus is still a matter of dispute. It would be interesting to know what clues may be afforded by the botany and by other branches of zoology to the time when Coiba was separated from the continent. Wetmore's ornithological reconnaissance should stimulate work in related fields.

EUGENE EISENMANN

MAMMALS OF THE ANGLO-EGYPTIAN SUDAN. *Proc. U. S. Nat. Mus., Vol. 106, No. 3377.*

By Henry W. Setzer. Smithsonian Institution. Washington. Free upon request (paper). Pp. 447–587; ill. 1956.

This important contribution to the mammalogy of Africa was inspired by the need of the U. S. Naval Medical Research Unit Number Three for a knowledge of the distribution of parasites infesting mammals of the Sudan. Most of the mammals studied were collected by personnel of the Unit. Also included in the report are data of all other Sudanese mammals, except bats, in the museum collections of America and in the British Museum, London. Presumably, the bats will be the subject of a separate report.

According to Setzer, the distribution of mammals

in the Sudan (the present name of the state) does not conform closely to the African biotic districts devised by Chapin on the basis of plant and bird distribution. Because of the similarity of their mammalian faunas, Setzer prefers to combine Chapin's Sudanese Arid and Sudanese Savanna Districts into what he now terms the Sudanese Arid Savanna District. Mammals of the remaining parts of the country show affinities with the fauna of the Somali Arid District, the Ubangi-Uelle Savanna District, and the East African Highland District.

Ninety-one genera of mammals, other than bats, are recognized. The vast majority of them are invaders from the south. Three rodent genera (gerbils, sand rats, jerboas) and the ibex are true Palearctic elements and reach their southern limits of distribution in the Sudan. Two genera of West African squirrels also find their eastern limits here. The grass hare (*Poelagus*) appears to be the only genus endemic to the region (including extreme northern Uganda).

The extraterritorial affinities and interrelationships of the 224 recognized species and subspecies of Sudanese non-volant mammals give a more intimate view of Sudanese ecology and the author's methods. It appears that no less in the Sudan than elsewhere in Africa, species inhabiting relict montane forests have differentiated most. Setzer accords at least subspecific rank to virtually all forms in each isolated forested area. In contrast, the Nile River, the most conspicuous topographic feature of Sudan, has had little appreciable effect on distribution. Generally, the mammals on both banks of the Nile are the same. Geographic variation along the river follows its course from north to south. Many of the smaller, sedentary species are represented by three, four, or even five races distributed along the main channel and its principal tributaries.

The subspecies recognized by Setzer are finely drawn and in many instances are probably local or seasonal variables. The status of each of a surprisingly large number of the species listed is so roundly hedged that it may be better to speak of them as "species." Setzer leans heavily on the characterizations, classification, and nomenclature of African mammals used by Ellerman, Morrison-Scott, and Hayman, but he berates them for what he regards as inordinate lumping. Much is gained by Setzer's criticism and reappraisals.

Organization and presentation of the data follow a standard form of provincial taxonomic reports. There is no key to the mammals. A few genera, notably those of the *Rattus* group, are perceptively diagnosed and their taxonomy clarified. Otherwise, there are no general descriptions or characterizations of species or higher taxons. Technical descriptions are restricted to types named for the first time. Measurements, however, are given for most of the specimens examined. Many annoying taxonomic problems regarding lesser Sudanese taxons are satisfactorily resolved, but none of this is really integrated with the systematics of African mammals in general. Notes on habits and habitats are rare and brief. The Sudan collecting localities are listed in a gazetteer, and the distribution of the species and subspecies is plotted on outline maps. For a notion of the geographic position of Sudan, its topography, ecology, and biotic zones, the student would do well to look elsewhere.

Mammals of the Anglo-Egyptian Sudan is definitely not a handbook for the amateur naturalist. The work was aimed at providing meticulously revised technical names of mammalian hosts of parasites. It appears that the successful attainment of this goal overrode whatever intentions the author may have had to discuss broader biological problems in more than perfunctory terms.

PHILIP HERSHKOVITZ

ECONOMIC ZOOLOGY

REPORT OF THE ATLANTIC HERRING INVESTIGATION COMMITTEE. *Bull. 3.*

By A. H. Leim et al. Fisheries Research Board of Canada. $3.50 (paper). viii + 317 pp.; ill. 1957.

The principal impetus to this exhaustive study was given in 1944 by the newly formed Atlantic Herring Investigation Committee in the following first sentence of their statement: "The herring fisheries of Atlantic Canada are a source of great wealth to the sea-washed provinces and Canada as a whole." During World War II interest developed in the greater utilization of the Atlantic sea herring, *Clupea harengus*, which is plentiful along the shores of the Gulf of St. Lawrence for periods of 4 to 6 weeks and then is absent for the rest of the year. This report describes the 5½ years of successful cooperation between the six provinces of Canada in the discovery of new stocks of fish and better ways of locating and catching them.

With the customary thoroughness and competence of Canadian scientists, the Committee attacked the problem from several broad fronts, resulting in much new and basic knowledge on the ecology of this species. Not since 1914–15, when the Canadian government retained various Danish fishery biologists, among them Johan Hjort and Einar Lea, to survey the herring resources of eastern Canada, has so much effort been expended on investigating the biology of this species in North American waters. A detailed study of the physical oceanography of the Gulf of St. Lawrence region, described in 7 of the 16 articles comprising this volume, was combined with old and new methods of hunting down the sea herring. Echo-sounders, purse-seines, drift-gill nets, and bottom and pelagic trawling were used to sample and exploit known and unknown stocks. The research was hampered at first by the lack

of a suitable boat, but later it was greatly amplified with the fully equipped 84-foot M. V. *Harengus*. Biological studies, represented in the 9 remaining articles, indicated the existence of several more or less distinct local populations that could be separated morphologically. Some of these stocks had never before been fully exploited.

This compilation is an excellent example of fishery science in action by North American workers. The Europeans have pioneered in the scientific exploration for fishery resources as well as for the same species of sea herring. Scientific research on this staple item of seafood has paid off handsomely again and again for the maritime countries of Europe. During its active life the Committee spent a little over $281,000 for the 6 year period. The report indicates that this was a small expenditure to make for such a rich store of facts, valuable to basic and applied aspects of the fisheries of the Western North Atlantic. Furthermore, it constitutes an important step towards the development of the very great potential herring fisheries of this region.

ROMEO MANSUETI

EINFÜHRUNG IN DIE HAUSTIERKUNDE. *Anatomie, Physiologie und Abstammung der Haustiere. 2. Auflage. By Hanns von Lengerken. Akademische Verlagsgesellschaft, Leipzig; Geest & Portig K.-G.* DM 12.– vi + 190 pp.; ill. 1954.

This book is a very elementary text dealing with the cellular nature, the gross anatomy, and the functions of the various organ systems of the farm animals. It can best be compared with many of the textbooks used in courses of hygiene in United States high schools and is apparently written for students similar to those in our schools of vocational agriculture. The nature of the cell and of cell division are described in a chapter of 3 pages; and the histology of the epithelium, muscle, nerves, blood, and bone, in only 9. The illustrations, although greatly simplified and diagrammatic, are numerous and give the reader a rather good idea of the skeletal system of cattle, the musculature of the horse, and the nervous system in general. The processes of digestion, excretion, circulation, respiration, and reproduction are briefly described.

F. N. ANDREWS

ANIMAL GROWTH AND DEVELOPMENT

THE BEGINNINGS OF EMBRYONIC DEVELOPMENT. *A Symposium organized by the Section of Zoological Sciences, A.A.A.S., and cosponsored by the American Society of Zoologists and Assn. SE. Biol., and presented at the Atlanta Meeting, December 27, 1955. Edited by Albert Tyler, R. C. von Borstel, and Charles B. Metz. American Association for the Advancement of Science, Washington.* $8.75 (AAAS members $7.50). viii + 400 pp.; ill. 1957.

More than a decade after he had abandoned the study and the world of embryology for other climes and other pursuits, von Baer made a visit to Italy; and while he was there, he almost returned to his first love, as he called her. He learned successfully how to fertilize the eggs of sea urchins artificially, and as a result of his studies wrote to a German colleague, "I am making a discovery which is, I believe at the heart (*Kern*) of embryology, and in view of which the mammalian egg seems to me only a feeble prelude." Nothing ever came of it, and with his return to St. Petersburg there came complete absorption in other than embryological research; but one wonders what seemed to him at the time more important than the discovery of the mammalian egg. Had it to do with fertilization? with nuclear or cytoplasmic division? These were all aspects of early embryology in which we know he was then interested. Alas, we shall never know. We do know, however, that an understanding of the earliest stages of development, which have never had a von Baer to open them to investigation, still lags greatly behind our comprehension of the phases to which he introduced us.

Both the intent and the content of this AAAS Symposium volume reflect the fact that it is the development of the adult from the egg rather than the development of the egg by the adult which embryologists commonly study. The contributors to the present compendium, which is both well conceived and well executed throughout, attempt in some minor degree to redress the balance, but the extent to which they are able to do so is limited by the absence of data in the neglected areas.

Cytogeneticists, to be sure, know a good deal about maturation from their own special point of view, but this still fails to inform us concerning the development of the particular qualities of the egg's cytoplasm which render it not only the most unique but also the most highly organized cell in terms of unrealized potentialities. Tyler writes in his Preface that "an understanding of early, as well as later, development depends largely on knowledge of the formation of the egg, that is, of the processes that endow the oocyte, in contrast to other tissue cells, with the capacity to form a new individual." Only one paper in the Symposium volume, that of W. S. Vincent, attempts to deal with this topic; and in his considerations of the origin and development of the oocyte, Vincent devotes himself particularly to the study of the role of the nucleus and of nucleolar ribose nucleic acid.

A number of sections deal with phenomena peculiar to fertilization. Arthur and Laura Colwin describe the morphology of spermatazoa, especially the production, structure, and function of the acrosome filament.

Charles B. Metz reviews the work concerning the reactions of specific egg and sperm substances, fertilizin and antifertilizin, and their possible functions in the activation of the egg. C. R. Austin and M. W. H. Bishop, in a chapter entitled Preliminaries to Fertilization in Mammals, consider the effects of the dilution of the ambient fluids on the motility of spermatozoa, the mechanisms of sperm transport and maintenance in the female genital tract, and the processes by which spermatozoa concentrate about and penetrate the zona; they conclude by describing briefly the reactions of the egg to penetration by the sperm. Another paper on mammalian fertilization, by M. C. Chang, takes up fertilization in vitro, activation, and parthenogenetic development, sperm penetration both from morphological and enzymatic points of view, the agglutination of spermatozoa, and the behavior of the pronuclei at fertilization. Alberto Monroy analyzes very briefly some changes in proteins of the sea-urchin egg at fertilization. Albert Tyler, in discussing Immunological Studies of Early Development, points out the new fact that an antiserum against fertilizin blocks both nuclear and cytoplasmic division in the young sea-urchin egg, and he discusses more generally recent studies on the development, detection, and morphogenetic significance of antigens and antibodies during development.

The remaining contributions treat aspects of development that involve later as well as earlier phases of morphogenesis. R. C. von Borstel's paper on nucleocytoplasmic relations in *Habrobracon* indicates that in this form the 6th or 7th cleavage is a critical period for mitosis, and presents some evidence from ultraviolet irradiation experiments which suggests that nucleic acid or nucleoprotein "perhaps in a particulate system, contains the information necessary for determinate development in the insect egg." H. E. Lehman reviews critically the work dealing with techniques and results of nuclear transplantation, particularly in amphibians. John Gregg discusses in a most thoughtful chapter the morphological and metabolic characteristics of gastrula-arrested *Rana pipiens* ♀ × *R. sylvatica* ♂ hybrids, and brings out the difficulties of relating the biochemical features of the hybrid embryos to their developmental peculiarities. John R. Shaver discusses the role of cytoplasmic particles during early development, particularly that of mitochondria in developing sea urchins. Silvio Ranzi reviews investigations of animalizing and vegetalizing substances and considers their effects on various embryos in terms of viscosimetric studies of proteins. G. Reverberi summarizes his work on the localization of enzymes in the ascidian egg.

Tyler has also pointed out in his Preface that the committee which planned the Symposium did not mean to imply by emphasizing the problems of early development that these were fundamentally different from those encountered in later development. Many of the papers enumerated in the immediately preceding paragraph, together with Tyler's chapter mentioned earlier, by tracing the continuity of events occurring before and after fertilization, underline the simple principle that it is the pre-fertilized egg which of necessity becomes the fertilized one. It is this principle which is the easiest to illustrate in studies of early development, and not only because of the greater amount of data available on post-fertilization stages which may serve as a point of departure for studies reaching into earlier phases of development.

It is an equally simple principle that fertilization results in change as well as continuity, and the abruptness of the change is perhaps the most dramatic aspect of the process from a morphological and physiological point of view. The suddenness of the change was what Frank Lillie called attention to when he drew his brilliant and soundly based analogy between the phenomena of fertilization and those of immunological reactions. It is his ideas which are still being exploited by the vigorous and highly significant investigations of morphogenesis by immunological methods and according to immunological concepts.

The fact that these studies have been and continue to be so abundantly fruitful should not delude prospective embryologists into the belief that studying fertilization as a specific reaction necessarily says all there is to know about qualitative differences between the fertilized and unfertilized egg. Are there no new ways, beyond the necessary demonstration of both abrupt and gradual changes in metabolic agents and their effects, to study the fertilization reaction itself? As far as the separate but related problem is concerned, that of studying the preparation of the egg by its maker, it is superfluous as yet to hope for new ways to attack it, since not even the old ones have been more than sporadically attempted. Yet it is clear that new questions, and not only the old familiar ones, must be asked of the potential egg before it is differentiated as an egg, if the mechanisms by which it realizes its potentialities at and after fertilization can be begun to be fully comprehended.

To return again to von Baer: "If the cells, that is the histological elements," he remarked in a footnote to his autobiography, "are to construct the animal organism on their own, they must have much morphogenetic intelligence." The embryo's intelligence concerning morphogenesis still transcends that of the embryologist. Von Baer was unique in his day for his emphasis, not only in his title but also in his working, on observation as well as on reflection. One of the present authors is almost as unique in our day for his reminder that clarification of the questions with which this Symposium was concerned must await further thinking as well as investigation. The volume is eminently useful in provoking such thought by treating so well of the knowledge that has been successfully acquired to date.

JANE OPPENHEIMER

NORMAL TABLE OF *XENOPUS LAEVIS* (DAUDIN). *A Systematical and Chronological Survey of the Development from the Fertilized Egg till the end of Metamorphosis.*

Edited by P. D. Nieuwkoop and J. Faber. Hubrecht Laboratory, Utrecht; North-Holland Publishing Company, Amsterdam. D. g. 22.75. vi + 243 pp. + 10 pl. 1956.

This is a systematical and chronological survey of the development of the Clawed Frog from fertilization until the end of metamorphosis. The 66 stages which the contributors recognize are made as comparable as possible to those established by Harrison for *Ambystoma maculatum* (*Amblystoma punctatum*). In addition, equivalents are shown in a table for 10 other species of frogs.

The descriptive accounts are a monument to international cooperation. The individual contributions, which were recast into book form by the editors, came from South Africa, the United States, Egypt, and six European countries. Financial support for publication came from the International Council of Scientific Unions.

Xenopus is widely used for pregnancy tests and for other hormonal studies. It is a specialized aquatic form generally regarded as remotely related to the rest of the extant frogs. It has a rather aberrant development but can be raised routinely in the laboratory. For these and other reasons, the descriptions will prove to be most helpful to a great number of diverse biologists.

A series of drawings illustrates the 66 stages, many from alternate views. There is an index and a bibliography of almost 1000 items.

ARNOLD B. GROBMAN

PARTHENOGENESIS AND POLYPLOIDY IN MAMMALIAN DEVELOPMENT.

By R. A. Beatty. Cambridge University Press, New York. $3.00. xi + 132 pp. + 2 pl.; text ill. 1957.

Many of the stock answers that students memorize in courses of cytology, genetics, and embryology are half-truths, e.g., that all of the cells of an individual possess the same chromosome number, that polyploidy cannot account for any part of evolution in animals utilizing sexual reproduction, or that mammalian embryos can form and develop only after the fusion of egg and sperm. A closer examination of existing data indicates that these assumptions either are not true, or that the subject should be viewed with an open mind.

The author, therefore, has explored the variations in normal development that occur, and that have been reported in the literature. These center around parthenogenesis and heteroploidy, and Beatty makes a sound plea for further investigation of these topics both by embryologists and cytologists. In summing up our present knowledge, he has shown that development, both normal and abnormal, can take any of numerous routes, but the principal question which he raises, "Can parthenogenetic or heteroploid mammals come to term?" is left unanswered. However, Kodani's data on human populations in Japan strongly suggest the existence of a certain measure of heteroploidy.

Beatty has done biology a service in bringing this subject into focus, and the book should pass across the desk of every serious student of development.

C. P. SWANSON

DEVELOPMENTAL CONCORDANCE AND DISCORDANCE DURING PUBERTY AND EARLY ADOLESCENCE. *Monogr. Soc. Res. Child Develop., Vol. XVIII, Ser. No. 56, No. 1. 1953.*

By Douglas M. More. Child Development Publications, University of Illinois, Champaign. $3.00 (paper). viii + 128 pp. 1955.

This report of research deals with the development of 33 adolescents. The author's endeavor is to discern some general interrelations between the temporal appearance of puberty, the maturation of social functioning toward peers and emotional maturation of attitudes tending toward adulthood. The group was admittedly not large enough to do more than afford an approximation to what might be found in some 60 per cent of high-school age persons in the United States. Striking differences in mode of development were found, as might be expected, between the two sexes. "Throughout . . . it was seen that the socially successful girl was the one who acted *as if* she were sexually mature, but who does not allow herself to feel the emotions which she appears to be acting out. Within the normal ranges of physical maturation in the sample, the girl who matures earlier has a distinct advantage in making this socially prized shift earlier." Among the boys, puberty is more gradual. "Sexual impulses are not forced completely out of consciousness and preconsciousness for them as they are for the girls . . . . The successful maneuver for the boy is to pretend he has no interest in members of the opposite sex, to divert his sexual energies into vigorous, gang-oriented behavior with other boys." Physiological changes, the established emotional life, the social group, and the societal forms and patterns constitute four major forces, the integration of which is the task of adolescence.

Although broad generalization from so limited a study is scarcely warranted, the study does possess interest for parents as well as child psychologists. Such individual case studies, when done with insight, have a definite place in human biology.

ANIMAL MORPHOLOGY

A TEXTBOOK OF HISTOLOGY. *7th Edition.*

By Alexander A. Maximow and William Bloom.

W. B. Saunders Company, Philadelphia. $11.00. viii + 628 pp.; ill. 1957.

The newest edition of this widely used and highly respected textbook of histology has incorporated a number of new illustrations as well as revisions in the text. Most of the changes have been aimed at bringing the material presented in a general histology course into line with recent experimental advances in the field. Most of these have necessarily been in the realm of the analysis of fine structure, by using improved instrumental methods such as the electron microscope, phase-contrast microscopy, polarized microscopy, etc. Some excellent electron micrographs, which will be meaningful to the student, have been included. All this has been accomplished without the unnecessary deletion of classical morphological information. These sections have been subjected to an intelligent revision; e.g., while the section on biliary passages has been condensed, information on the more recently discovered hormones and advances in immunology has been added. Although some detail has been cut to balance with the material added, the treatment still represents the most detailed account of vertebrate histology available in a textbook in the English language. With developments moving at their present pace in the area of the analysis of submicroscopic structure, such a revision, incorporating information from this area that may be assimilated in a general histology course, is indeed welcome.

RONALD R. COWDEN

PRATIQUE ANATOMO-PATHOLOGIQUE. II. MICROSCOPIE. *Deuxième Édition By J. Delarue, P. Gauthier-Villars, F. Busser, and Ch. Gouygou. Masson & Cie., Paris.* 1800 fr. 337 pp.; ill. 1957.

The basic organization of this book is in the form of double-page spreads. Each right-hand page illustrates the affected tissue and the left-hand page describes it under the headings of the general appearance of the tissue or organ and the appearance of the lesion itself. A brief résumé closes the text. A great deal of information is included in very restricted space. Such a volume as this should be useful to pathologists who have occasion to refer to a very brief account of a wide variety of lesions.

F. N. LOW

LE POUMON. *Structures et Mécanismes à l'État Normal et Pathologique. Second Edition. By A. Policard. Masson & Cie., Paris.* 1,500 fr. (paper). 263 pp.; ill. 1955.

The second edition of this monograph has been extensively reworked and parts of it have been rewritten since 1939, when the first edition appeared. However, the organization of the work has not been radically changed. The first part contains 12 chapters on the normal lung and 3 on diseased conditions. The second part, consisting of 4 chapters, deals with the broncho-vascular apparatus, including the lymphatics.

A good deal of information on the lung will be found in this monograph, but it is not without the shortcomings so frequently encountered in many such publications. Meticulous attention to recently published investigations characterizes the work of European scholars. But, in the present volume, these citations stand in disharmonious contrast to a tenacious unwillingness to modify established opinions in keeping with new discoveries. It appears, in this connection, that dynamic interpretation of new discoveries is strongly inhibited by the popular belief that admission of erroneous opinion in previously published work is the capital crime of scientific investigation. For example, electron microscopy has demonstrated a continuous epithelial lining on the alveolar wall. This has been verified in numerous laboratories and is generally accepted in America, having found its way into at least three leading textbooks. But, although the author cites recent investigations utilizing electron microscopy, he describes the alveolar wall as "naked," the view he supported before the advent of electron microscopy. And the few electron micrographs reproduced which show the area in question are, by modern standards, of unacceptable quality.

But shortcomings such as this apply largely to controversial subjects about which there may reasonably be expected to be a residual difference of opinion. In the main, the content of this monograph is reliable, and it is recommended to the specialist seriously interested in lung structure.

F. N. LOW

RECHERCHES SUR LA CONSTITUTION DE L'OS ADULTE. *By J. Vincent. Éditions Arscia, Bruxelles.* 200 B.fr. (paper). 153 pp.; ill. 1955.

This monograph, a dissertation presented to the medical faculty of the Catholic University of Louvain, emanates from the laboratory of P. Lacroix, whose excellent book on the organization of bone is a classic in its field. Histologists are coming to realize that adult bone is a living plastic structure which is constantly in the process of destruction and replacement, rather than the permanent sort of thing imagined for many years. The present work is based on this premise and the author cites the work of Tomes and De Morgan who, in 1853, described bone in exactly this way, only to have it be forgotten by histologists in general for nearly a hundred years.

In keeping with this dynamic concept, microradiography is extensively used to follow the progress and

distribution of such elements as calcium and sulfur in bone structure. Both compact and spongy bone in animals are subjected to separate analyses. Human bone has received less attention. There is a general discussion of pertinent questions and an extensive bibliography. The illustrations, in halftone, are good.

This is clearly a book for the specialist. But it is of high quality and should be in the library of all scholars seriously interested in bone.

F. N. Low

A Laboratory Guide to Anatomy and Physiology.
By Barry G. King and Mary Jane Showers; illustrations by Phyllis Anderson. W. B. Saunders Company, Philadelphia and London. $3.00 (paper). xii + 161 pp.; ill. 1957.

This volume is designed for use in an undergraduate course in college or nursing school. Its sections are devoted to the body as an integrated whole, nervous control, muscular activity, metabolism, and reproduction. Line drawings suitable for labeling are supplemented by text and instructions. The pages are perforated for tearing out and punched for inclusion in a looseleaf notebook. The format is neat and the contents clear. This is a good book of its kind.

F. N. Low

ANIMAL PHYSIOLOGY

Recent Studies in Avian Biology.
Edited by Albert Wolfson; 13 contributors. University of Illinois Press, Urbana; published under the sponsorship of the American Ornithologists' Union. $7.50. x + 479 pp.; ill. 1955.

Whether it is best to collect reviews of biological researches on the basis of their unity of experimental approach or on the basis of the type of organism may be left to the user to determine. We are accustomed to the former—*Advances in Genetics, Recent Progress in Hormone Research, Symposium on Amino Acid Metabolism,* etc. Now comes the other sort of grouping, *Recent Studies in Avian Biology.* The contents cover a wide scope; the contributors are outstanding workers in their respective areas. Contents: Concepts and Problems of Avian Systematics in Relation to Evolutionary Processes (Alden H. Miller); Recent Revisions in Classification and their Biological Significance (Herbert Friedmann); Paleontology (Alexander Wetmore); Avian Anatomy, 1925–50, and Some Suggested Problems (Harvey I. Fisher); The Study of Behavior in Birds (John T. Emlen, Jr.); Bird Navigation (Donald R. Griffin); The Annual Stimulus for Migration: Experimental and Physiological Aspects (Donald S. Farner); Direct Studies of Nocturnal Bird Migration (George H. Lowery, Jr., and Robert J. Newman); Breeding Biology of Birds (David E. Davis); Recent Advances in Knowledge Concerning the Role of Hormones in the Sex Differentiation of Birds (L. V. Domm); Some American Population Research on Gallinaceous Birds (Joseph J. Hickey); Birdbanding in the Study of Population Dynamics (Donald S. Farner); Diseases of Birds (Carlton M. Herman).

The book is beautifully printed. It is a singular fact that there is not one picture of a bird in it.

The Physiology of Nerve Cells.
By John C. Eccles. The Johns Hopkins Press, Baltimore. $5.75. ix + 270 pp. + 2 pl.; text ill. 1957.

The Herter Lectures for 1955, given by the author at The Johns Hopkins University, have been considerably expanded here into an extensive account of the nature of synaptic transmission in the central nervous system, on the basis of an ionic hypothesis. This hypothesis, which has recently been so successful in the hands of Hodgkin, Huxley, Katz, and Keynes in explaining the nature of nerve conduction, is based on the concept that the events of excitation consist of a sequence of changes in ionic permeability of the cell membrane. Eccles and his collaborators have applied the hypothesis with remarkable success to spinal motoneurons of the cat. Their thesis is the following: The primary event at the synapse is the production of a transmitter substance which diffuses across the synaptic cleft to the subsynaptic membrane of the postsynaptic cell. The transmitter substance then causes changes in the ionic permeability of the subsynaptic membrane. At an excitatory synapse the membrane becomes highly permeable to all ions, a state leading to a depolarization of the soma. At an inhibitory synapse the membrane becomes highly permeable to potassium and chloride, but not to ions as large as sodium, so as to repolarize the soma if it has become depolarized as a result of activity at excitatory synapses. The degree of depolarization of the motoneuron thus depends upon the relative predominance of excitatory over inhibitory activity among the synapses impinging on the cell. If the depolarization reaches threshold level, the cell will discharge one or more impulses. In order to prove their thesis, Eccles and his collaborators have made elegant use of a double-barrelled micropipette inserted into the cell body. With it they were able to measure the absolute membrane potential through one barrel while using the other barrel either for passing polarizing currents or for electrophoretic injection of ions. They were consequently able to produce a wide variety of effects, all of which could be fitted into the framework of their hypothesis.

Eccles devotes the major part of the book to these experiments and is able to explain an impressive number

of observations on spinal cord excitation. The experimental demonstration that inhibitory synaptic action tends to restore the membrane potential of the motoneuron soma to a near resting level puts our knowledge of central synaptic action on a new plane. He also devotes considerable space to the work of other investigators who have found similar results on other preparations. Especially noteworthy is the work of Kuffler and Eyzaguirre on a crustacean stretch receptor cell. In the last two chapters certain relevant fields are reviewed, including a discussion of types of pathways in the central nervous system in relation to possible transmitter substances involved in the various inhibitory and excitatory actions, and a variety of special topics ranging from the possible sieve-like structure of the subsynaptic membrane to reactions of nerve cells that bear on the phenomenon of memory. The book is very condensed and requires considerable reference to the original papers for a thorough understanding of its contents. The author has been most helpful in this regard by his extensive documentation throughout.

PHILIP W. DAVIES

NORADRENALINE. *Chemistry, Physiology, Pharmacology and Clinical Aspects. American Lecture Series, Pub. No. 261.*

By U. S. von Euler. Charles C Thomas, Springfield, Ill. $11.50. xxii + 382 pp.; ill. 1956.

Noradrenaline, although on the chemists' shelves since it was synthesized by Stolz in 1904, was not recognized as a natural constituent of the animal body until 1946, when P. Holtz in Germany and U. von Euler in Sweden separately directed the attention of physiologists to its importance. The present valuable monograph systematically assembles existing information on its nature, occurrence, and function. The bibliography lists some 750 publications, most of which have appeared since 1946. As stated by Sir Henry H. Dale in a Preface, "There can seldom have been a case in which a substance, with no more than a restricted claim to special importance in therapeutics, . . . has attained so rapid a celebrity . . . The interest which it has attracted is due of course, not merely to the discovery of its natural occurrence, but largely to the implication, and the eventual endorsement of this by direct evidence, of its important functions in the animal body, and especially of its action as the predominant chemical transmitter of the effects of adrenergic nerve impulses, mainly in postganglionic sympathetic nerve fibres, to the effector cells in contact with which such fibres end." This volume is a monograph in the Bannerstone Division of the American Lectures in Physiology, edited by Robert F. Pitts, who has in this instance made a most worthwhile selection.

EVELYN HOWARD

THE PHYSIOLOGY OF THE PITUITARY GLAND OF FISHES. *By Grace E. Pickford and James W. Atz. New York Zoological Society, New York.* $6.00 (paper). xxiii + 613 pp.; ill. 1957.

The most impressive feature of comparative endocrinology is the similarity of endocrine functions among the vertebrates. Many uncertainties and limitations, nevertheless, have existed in our knowledge concerning basic features of pituitary gonadotropins, especially among the lower craniates. This prodigious work, a critical review of the world literature on the target organ of the endocrine system in lampreys, sharks, rays, and bony fishes, fills in many of the lacunae in our knowledge. The primary objectives are to make available in one volume carefully digested and authoritative information on the subject and to discuss in detail many of the problems concerned with fish pituitary hormones.

Considerable advances have been made in fish endocrinology during the last decade. Much of the published material is scattered in the world literature, some of it out of reach of many workers. Little of it heretofore has been assembled for critical analysis for American students. The authors have drawn a readable and coherent picture of the complex nature of this gland from the massive and polyglot literature.

Endocrinologically, cyclostomes, dipnoans, and chondrosteans are regarded as primitive. Teleosts and elasmobranchs are highly specialized and are regarded as being as "modern" as any of the so-called higher vertebrates in their endocrine systems. The evidence suggests that endocrine functions ancestral to the tetrapods are apparently not found in elasmobranchs and teleosts, as earlier writers generally speculated to be the case. These general remarks, of course, hardly suggest the range of subject matter covered in the publication. The following broad topics are discussed in detail: hormones of the neurohypophysis, chromatophore-regulating hormones of the pituitary, the adrenal and corticotropin, the growth hormone, the thyroid and thyrotropin, miscellaneous and unclassified functions of the pituitary, the technique of hypophysectomy in fishes, and the relation of the pituitary to reproduction in fishes. Necessary background information is presented for an evaluation of the results of experiments on fish pituitary physiology and regulation. In spite of the vast literature reviewed, it is concluded that knowledge is still so meager that generalizations on the endocrines for all fishes are not justified at present.

The authors acknowledge aid and counsel from over a dozen authorities, many of whom had contributed elsewhere much of the basic data presented in the book; yet much original material is also included. The work is accompanied by a carefully collated bibliography of 1905 items of the world literature, of which 165 are Russian. All titles contain page references to citations in the text and tables. Appropriately, the work is dedicated to Professor Alexander Petrunkevitch, who translated

over 100 of the Russian papers cited in the text. Brazilian and Japanese papers also contribute significantly to the full treatment of the subject. From the standpoint of practical fish-cultural application by treating fishes with gonadotropic hormones in order to induce reproduction in captivity, the U. S. S. R. and Brazil have been the pioneers in this field. All known experiments, up to June 1956, concerning the pituitary gland and pituitary physiology of fishes, are summarized in 54 detailed tables.

The book is indeed a model of its kind. It will easily serve as a complete reference work on the subject for some time to come. Just enough introductory material is given in each subject to permit use by workers with a wide range of backgrounds. Definitions are clearcut; and detailed cross-indices will facilitate use of the book. More important, it should open up new vistas for ichthyologists and fishery biologists working on fish eggs and larvae in hatcheries, and on many problems of piscine physiology. Comparative physiologists and endocrinologists, in general, will find it most useful, but it holds unique value for fishery scientists and fish culturists.

ROMEO MANSUETI

LA FONCTION OVARIENNE ET SON EXPLORATION.
By R. Vokaer. Masson et Cie., Paris. 850 fr. (paper). 108 pp.; ill. 1956.

This monograph is directed primarily to the clinician. In 3 brief chapters it scans the subject, including the embryonal development, postnatal and adult ovary, in addition to ovogenesis, menstruation, ovulation, and the gonadal hormones. The fourth chapter, which covers more than half the monograph, deals with technics for the examination of ovarian function and includes: history-taking; temperature-charting; the histological examination of the endometrial and vaginal mucosa; and the cytology of vaginal contents, in addition to study of the vaginal flora, pH, glycogen, and cervical mucus. Vokaer finally touches on biological and chemical assays for the determination of estrogens and progesterone. An appendix of synoptic charts for utilizing different tests in exploring ovarian function for major pathology completes the work.

The scope of the subject which the author set for himself is heroic, and in a short monograph he can mention only keynotes. The selection of material is an especially difficult task, but Vokaer has succeeded in giving the clinician a panoramic view which should permit an interested reader to explore various regions at closer range.

The bibliography of 128 citations (including 8 books) is drawn almost entirely from clinical journals, and 77 are from French language publications. The literature is mostly of 1946–1954 (107 citations). There are many illustrations and tables.

M. C. SHELESNYAK

GESTATION. *Transactions of the Third Conference: Mar. 6, 7, and 8, 1956, Princeton, N. J.*
Edited by Claude A. Villee. Josiah Macy, Jr. Foundation, New York. $4.75. 253 pp. + 1 chart; ill. 1957.

Whereas the first and second Macy Conferences on Gestation were concerned with placentation, and with the physiology of the fetus and placenta, the recently published Third Conference is devoted, in the main, to the endocrinology of gestation. This subject is attacked from two broad points of view: (1) maternal and placental hormones and their effects during pregnancy, and (2) the endocrine activities of the fetal glands.

Gregory Pincus introduces the topic of maternal endocrine secretions by pointing out some of the major gaps in our knowledge of hormonal control of ovulation, the uterine endometrium and implantation, and hormonal effects on the developing fetus. He also reviews his work on steroidogenesis in the placenta and indicates the importance of pituitary gonadotropin in the latter part of pregnancy. The reports of Eleanor Venning, M. X. Zarrow, and Roy O. Greep discuss the significance of other maternal hormones on pregnancy and parturition. Of some note is the interesting discussion by Zarrow of the luteal hormone "relaxin."

There can be no doubt that fetal endocrines are functional during much of intra-uterine life, and that fetal tissues are sensitive to hormonal influences. The report by Alfred Jost on the relation between the fetal pituitary and thyroid glands, on endocrine effects on glycogen storage in the fetal liver, and on hormone secretion by the fetal testis not only bears out such a conclusion, but also contributes to our knowledge of gland–hormone–target-organ relationships. Lemen J. Wells describes his attempts to seek out such relationships in the "extra-uterinized" rat fetus by extirpating one or another gland and injecting purified hormones. An even greater degree of experimental control is obtained by Dorothy Price, in her cultures of differentiating rat reproductive tracts, in vitro. In this preparation, in which unknown or uncontrolled variables are minimized, the morphogenetic effects of fetal male hormone are clearly demonstrated. Hormonal effects, as manifested in the rat estrous cycle, are explored by Curt P. Richter, with special emphasis on stress and amygdaloidectomy, while Emil Witschi discusses the etiology of gonadal agenesis and sex reversal.

Of especial interest, at least to this reviewer, is the report by Claude Villee, summarizing his recent work on estradiol regulation of oxygen metabolism in the

human placenta. Working with tissue slices, homogenates, and finally, with particle-free extracts, Villee was able to trace the site of action of the hormone to the Krebs-cycle enzyme, isocitric dehydrogenase. The activity of this DPN-linked enzyme can be approximately doubled by appropriate concentrations of estradiol. This finding represents one of not more than three or four examples in the literature, of a definite link, at the biochemical level, between a hormone and its physiological effect.

The Transactions of the Macy Conferences, in which the informal reports and open discussion are published essentially verbatim, are obviously not suited as textual material. Factual data are not easily located, and the logical development of concepts is frequently interrupted as questions or new ideas are thrown into the discussion. However, for persons with some background in the subject, these transactions provide valuable insights into the ideas and thinking processes of some of the leading workers in the field.

ROBERT L. DEHAAN

PHYSIOLOGY OF PREMATURITY. *Transactions of the First Conference, March 21, 22, and 23, 1956, Princeton, N. J.*

Edited by Jonathan T. Lanman. The Josiah Macy, Jr. Foundation, New York. $3.25. 151 pp.; ill. 1957.

This conference, held in March 1956, covered two general topics, fetal-maternal endocrinology in late pregnancy, and the fetal and placental circulation in late pregnancy. As stated by the chairman, Clement A. Smith, it is the purpose of these conferences to generate ideas to take home and think about. There is in the record a minimum of formal presentation of factual material. However, although the resulting soup seems rather thin at times, it is of excellent and intriguing flavor.

EVELYN HOWARD

ENVIRONMENTAL PHYSIOLOGY OF ANIMALS.

By William S. Hoar. Scholar's Library, New York. $2.25 (paper). viii + 91 pp. 1956.

In this laboratory manual of environmental physiology the organism is studied largely in terms of reaction to the environment. The initial experiments appropriately concern permability. Studies of water balance, gas exchange, temperature and the like follow. The experiments described are simple, likely to be successful in student hands, and aptly illustrate the principles under consideration. While the manual is undoubtedly well suited to the pedagogical niche intended by the author, that of an introduction to experimental zoology for students of applied zoology, it appears unsuitable to the general university curriculum. Its subject material is ordinarily well covered in a beginning physiology laboratory.

J. F. CASE

FUNDAMENTALS OF IMMUNOLOGY. *Third Edition, revised and rewritten.*

By William C. Boyd. Interscience Publishers, New York and London. $10.00. xiv + 776 pp.; ill. 1956.

The appearance of three editions of this textbook within 13 years not only reflects the many recent advances made in immunology but also attests the popular demand for this book. Since it was intended by the author to supply an introductory text to both student and researcher rather than a complete treatise on the subject, certain specialized topics have been omitted or only briefly mentioned in favor of a more complete discussion of basic principles. However, the material presented, both factual and theoretical, is amply supported with bibliographic references, and the current concepts are described and evaluated without losing sight of the colorful historical background of the subject. The book thus nicely fills the need for a desk reference for those in allied biological and medical fields who from time to time are confronted by research problems involving immunology.

This edition is not only revised but has been extended by several new chapters. One, of particular current interest, is devoted to autoimmunization, a fundamental problem in understanding the etiology of "idiopathic" blood diseases and probably many other unexplained pathologic states. Another new section deals with practical applications of the subject in medical practice. Also of importance, particularly to those not trained in immunology, is an entire chapter given to immunologic tests and preparations. Most of these are described in detail, including mathematical treatment and expression of test results. This book is, without doubt, an excellent medical and graduate text in the principles of immunology.

THOMAS E. NELSON, JR.

ANIMAL NUTRITION

VITAMIN B12 UND INTRINSIC FACTOR. *1. Europäisches Symposion über Vitamin B12 und Intrinsic Factor, Hamburg 23.–26. Mai 1956.*

Edited by H. C. Heinrich. Ferdinand Enke Verlag, Stuttgart. DM 75.–(paper); DM 79.–(cloth). xvi + 576 pp. + 3 pl.; text ill. 1957.

This book is a collection of the papers given at the first International Symposium on problems relating to Vitamin B12 and the Intrinsic Factor. As would be

expected, some of the papers are in French and German, but the majority have been printed in English. Not only the wide diversity of subjects covered by these papers, but the extensive lists of references accompanying most of the articles make this work an invaluable source to anyone interested in this field. Both the basic and clinical aspects of current problems concerning the etiology and treatment of deficiency states, as well as the metabolic role, absorption, utilization, and excretion of Vitamin B12, are reviewed.

The sections in the first half of the symposium are on chemistry and biosynthesis of Vitamin B12 compounds, the biochemical mechanism of the action of Vitamin B12, the Intrinsic Factor and Vitamin-B12-binding factors, and methods of bioassaying Vitamin B12. The remarkable progress made in the past few years in knowledge regarding the chemical structure and the important metabolic roles of this essential human nutrient are reviewed in these papers. The many still unsolved problems relating to the details of its metabolic action and its natural relation to Intrinsic Factor are clearly indicated.

Of particular interest in these sections on the basic properties of Vitamin B12 are papers by H. R. V. Arnstein and B. Connor Johnson which clearly review progress made to date in understanding the role played by Vitamin B12 in the metabolism of one-carbon units and the role of Vitamin B12 in animal nutrition. H. G. Wigmenga and R. F. Schilling, in two further papers, review clearly and completely our present knowledge, including their own recent studies on the problem of the Intrinsic Factor and Vitamin B12 absorption binding.

The second half of the symposium deals with clinical problems relating to Vitamin B12 deficiency and covers a wide range of loosely related subjects. W. F. Alexander, K. L. Zirm, B. San-TJiang, G. Astaldi, and others present a series of papers covering the detailed pathological changes of various tissues resulting from Vitamin B12 deficiency. D. L. Mollin and his coworkers review in 3 papers the work with serum Vitamin B12 levels and radioactive Vitamin B12 in a variety of diseases associated with megaloblastic anemia. They also present in some detail their own interesting studies on the absorption of labelled Vitamin B12.

Altogether, this appears to have been a valuable international interchange between workers in this field, and the publication of the papers presented gives us one of the most concise yet complete summaries to date of the entire field.

PATRICIA A. MCINTYRE

BIOPHYSICS AND GENERAL PHYSIOLOGY

PHYSICAL TECHNIQUES IN BIOLOGICAL RESEARCH. *Volume II. Physical Chemical Techniques. Edited by Gerald Oster and Arthur W. Pollister. Academic Press, New York.* $12.80. xv + 502 pp.; ill. 1956.

The second of this series of 3 volumes, devoted to physical techniques which have been found useful in biological research, is concerned largely with those techniques which have been used to investigate the properties and structure of molecules of biological importance. Each technique is treated in a separate chapter by a recognized authority. The subjects covered, with their authors, are as follows: Tracer Techniques (Jacob Sacks); Measurement of Ionizing Radiation (J. S. Kirby-Smith); Sedimentation, Diffusion, and Viscosity (A. G. Ogston); Surface Film Techniques (Alexander Rothen); Absorption and Chromatography (N. Applezweig and T. F. Cleary); Electrophoresis (K. Stern); Electrical Potential Differences (K. S. Spiegler and M. R. J. Wyllie); Magnetic Methods (Scott Blois); and X-ray Diffraction and Scattering. In most cases the subject is treated in detail, and extensive bibliographies are given.

FRANCIS D. CARLSON

pH MEASUREMENTS. *By Victor Gold. John Wiley & Sons, New York.* $2.25. 125 pp.; ill. 1956.

This book was intended to help the non-specialists understand the concept of *p*H and also the significance of the measurements. The author has succeeded in these goals. Sufficient basic information necessary to understand the definitions and methods of measurement is included. The various *p*H scales and the interrelationships between them are clearly defined. Two chapters deal with *p*H measurements by E.M.F. and optical methods. Titration curves and buffer solutions are considered in sufficient detail to provide the reader with the basic information for the understanding of these topics. Lists of *p*H standards, with their compositions, form part of the appendices. The mathematical symbols used in the book are collected in a table, and this table includes reference to the page containing the definition of the symbol. This should be of great assistance to those with little familiarity with the subject. Practical hints about such items as buffer solutions and electrodes are interspersed in the text, but the book cannot be regarded as a substitute for a practical manual. This little volume provides a place where one can renew and review his understanding of those basic elements upon which *p*H measurements rest.

LEOPOLD MAY

DIE PHYSIKALISCHE GRUNDLAGE DES LEBENDEN SYSTEMS (ATOM UND MOLEKÜL). *Grundlagen der allgemeinen Vitalchemie in Einzeldarstellungen. Band I.*

By Karl Kaindl; introduction by Hans Linser. Urban & Schwarzenberg, Wien. DM 32.–(paper). viii + 201 pp.; ill. 1955.

DIE PHYSIKALISCH-CHEMISCHEN GRUNDLAGEN DES LEBENDEN SYSTEMS. *1. Die Vereinigung von Molekulen zu Ordnungszuständen. 2. Die chemische Reaktion. Grundlagen der allgemeinen Vitalchemie in Einzeldarstellungen. Band II.*

By Karl Kaindl and Stefan Holzel. Urban & Schwarzenberg, Wien. DM 31.–(paper). vi + 138 pp.; ill. 1956.

These volumes provide the basic physical chemistry to be used in the succeeding volumes. The same material is found in most standard physical chemistry textbooks.

LEOPOLD MAY

LIGHT SCATTERING BY SMALL PARTICLES.

By H. C. van de Hulst. John Wiley & Sons, New York; Chapman & Hall, London. $12.00. xiii + 470 pp.; ill. 1957.

The book is primarily a presentation of the basic theory of the light-scattering phenomenon. The author has compiled the data from the literature, and wherever necessary has extended the calculations. The first part of the book contains the basic theory necessary for an understanding of light scattering. The second part presents the problems of mathematical physics which deal with the properties of the single particle. The last section is concerned with specific fields of applications, and one chapter is devoted to chemical applications. Although this book gives the biologist few direct solutions, it does provide the basic information and techniques to solve his own particular problems. For those interested in the basic theory and methods of solving problems of light scattering of particles of any size, this book is a valuable source.

LEOPOLD MAY

BIOCHEMISTRY

UNSTABLE CHEMICAL SPECIES: FREE RADICALS, IONS, AND EXCITED MOLECULES. *Ann. N. Y. Acad. Sci., Vol. 67, Art. 9.*

Edited by Otto v. St. Whitelock. The New York Academy of Sciences, New York. $4.00 (paper). Pp. 447–670 + 1 pl.; text ill. 1957.

This collection of papers includes discussions of methods for the study of unstable chemical species and results obtained with various types of materials. Of particular interest to the biochemist are two papers on the role of free radicals in organic reaction mechanisms and biological oxidations. The first report is a review of the subject. The second paper deals with free radical formation during enzymatic oxidation of 2-electron oxidizable substrates. The formation of free radicals in water by ionizing radiations is illustrated in producing coupled oxidation-reductions between biological systems. This book is a good reference volume for one interested in various methods for investigating free radicals.

LEOPOLD MAY

THE HARVEY LECTURES. *Series 51 (1955–1956). Delivered under the Auspices of the Harvey Society of New York, under the Patronage of the N. Y. Acad. Med.*

Academic Press, New York. $7.50. xiv + 298 pp.; ill. 1957.

The 1955–56 Harvey Lectures, in keeping with earlier series, includes a group of essays by distinguished biologists working at the growing edges of experimental endeavor. What they have to say on their particular problems is, therefore, both pertinent and timely. Since the talks are directed to a general rather than to a special audience, they are of particular interest to those working in related disciplines who would like to keep in touch with what their colleagues are doing. The general tone and level of the series can best be gained by a listing of the authors and their topics: Eccles on synaptic phenomena; Gale on nucleic acids and protein synthesis; Fruton on the hydrolysis and synthesis of peptide bonds; Meyer on the chemistry of mesodermal ground substance; Rammelkamp on streptococcal infections; Racher on cycles in carbohydrate metabolism; Hershey on bacteriophage; and McElroy on bioluminescence.

The emphasis consequently is biochemical and physiological, but where frontiers are being pushed back, and mechanisms are being analyzed, this trend is inevitable, and, indeed, is indicative of the sophistication of current research.

C. P. SWANSON

BIOCHEMISTRY AND THE CENTRAL NERVOUS SYSTEM.

By Henry McIlwain. Little, Brown & Company, Boston. $9.50. viii + 272 pp.; ill. 1955.

The author, who teaches at the University of London, states that every year some 3000 papers appear which concern chemical substances or processes and the central nervous system. To cull the significant from this enormous scientific production and then reduce it not only to manageable proportions but to a coherent, comprehensible treatment is a task few would dare to undertake. That the author has been so successful is sufficient tribute. He has managed to provide the necessary unity by keeping the nature of the biochemi-

cal mechanisms involved in brain metabolism at the focus of his treatment. He starts with brain metabolism in situ, discusses the chemical composition of the brain, then takes up the metabolism of brain slices and other portions removed from the body, and finally comes to the metabolism of homogenates and cell-free cerebral systems. Four chapters then deal with chemical aspects of metabolism: pyruvate metabolism and oxidative phosphorylation; amino acids; vitamins; and cerebral lipids. A chapter on cytochemical and histochemical aspects leads into a consideration of the chemical and enzymic make-up during embryonic development. Two chapters consider acetylcholine, sympathin, and related substances; and depressants and excitants of brain function. The last chapter deals with rates of chemical change in the brain. The relatively small size of the book is one of its chief merits, since it will enable workers in other fields to gain some perspective in this important and rapidly expanding subdivision of biochemistry.

BENTLEY GLASS

BIOCHEMISTRY OF AUTOTROPHIC BACTERIA.

By Howard Lees. Butterworths Scientific Publications, London. 21s. viii + 112 pp.; ill. 1955.

Lees has commented elsewhere that the treatment of the biochemistry of many autotrophic systems is not inherently difficult, but nonetheless scarcely exists. The present work is a fairly elementary introduction to the biochemical problems of autotrophy in bacteria, with special emphasis on nitrifying, hydrogen-oxidizing, and non-photosynthetic sulfur bacteria. It might best serve university students as a preparation for the more detailed (and fragmented) treatments, e.g., in the Society for General Microbiology Symposium on *Autotrophic Microorganisms*.

The author recognizes the difficult question whether the biochemistry of autotrophy can, at this stage, be set apart from other aspects of microbial metabolism. To attempt to "bring some order into the apparently chaotic biochemistry of these organisms" he sets forth a hypothetical evolutionary scheme. On the postulates that little organic material was initially present, and that the oxygen in the atmosphere is of photosynthetic origin, it would follow that the primeval organisms would have been anaerobic photosynthesizers—in fact rather like the purple non-sulfur bacteria. The mutational loss of different capacities would lead to the biochemical diversification now exhibited by microbial types. The postulation of photosynthesis as a primitive attribute is widely accepted, but is it a necessary one in the light of the arguments by Oparin and others for the abiotic accumulation of organic molecules?

J. LEDERBERG

THE CHEMISTRY OF PLANTS.

By Erston V. Miller. Reinhold Publishing Corporation, New York; Chapman & Hall, London. $4.75. vii + 174 pp.; ill. 1957.

The *Chemistry of Plants* attempts to condense into a single small volume a tremendous amount of information about the organic and inorganic composition of plants. The chapters on hormones, glycosides, and alkaloids are quite useful, but the chapters on carbohydrates, lipids, amino acids, organic acids, and enzymes are rather out of date. For the most part, they could have been written fifteen or twenty years ago. The most serious shortcoming of this book is its lack of adequate references. Virtually every chapter has been the subject of some recent textbook, but none of these recent writings is mentioned.

G. R. NOGGLE

THE STRUCTURE OF NUCLEIC ACIDS AND THEIR ROLE IN PROTEIN SYNTHESIS. *Biochem. Soc. Sympos., No. 14.*

Edited by E. M. Crook. Cambridge University Press, New York. $3.75. 74 pp. + 2 pl.; text ill. 1957.

In a field which moves so rapidly, otherwise useful collections may soon become outdated or superseded. A far better book to buy, which covers the same material and much more besides, is the contemporaneous *Symposium on the Chemical Basis of Heredity*. If small collections of this sort cannot be produced more economically, one may seriously wonder whether the brief monograph is still a useful vehicle of publication.

As to the actual contents of the Biochemical Society Symposium, it contains papers by Markham and Wilkins on the structure of nucleic acids, and by Burton, Gale, and T. S. Work and colleagues on protein synthesis by phage, bacteria, and animal tissues respectively. There is unhappily still no single biological system in which one can verify the tacitly assumed transfer of information from DNA → RNA → protein, and until this has been found the links are shaky. I applaud Pirie's suggested resuscitation of "nuclein" as a generic term for "purine or pyrimidine."

J. LEDERBERG

MICROBIOLOGY

ZINSSER'S BACTERIOLOGY. *Eleventh Edition.*

By David T. Smith et al. Appleton-Century-Crofts, New York. $12.00. xiii + 953 pp. + 100 tables; ill. 1957.

The new edition of Zinsser's standard text will help to strengthen its position among the top choices

(Jordan-Burrows and Dubos-Rivers are others) for the teaching of medical bacteriology. The 2-column format, numerical handling of references, and addition of some recently published electron micrographs improve its readability, important since medical students generally favor the inadequacies of their own lecture notes to the reading of a reliable text. The nomenclature of Bergey's 7th Edition has been adopted, and information on antibiotic susceptibility has been included. Perhaps most welcome are the extensive revisions of important introductory portions on immunology (including a new chapter on the human blood groups and immunohematology), cytology, and the physiology of microorganisms.

PHILIP E. HARTMAN

ANNUAL REVIEW OF MICROBIOLOGY. *Volume 10. Edited by Charles E. Clifton; associate editors, Sidney Raffel and Roger Y. Stanier. Annual Reviews, Palo Alto.* $7.00. viii + 426 pp.; ill. 1956.

This series of annual reviews is becoming—what it has not always been—an indispensable treat, with something for any microbiologist. One author baldly asserts that his "article is an essay rather than a review," an approach for which no apologies are needed.

A new feature in this issue is P. Grabar's review of work in the U.S.S.R. He found "a predominance of works undertaken for an immediate practical purpose." Lysenkoistic doctrines evidently still pervade (and confuse) basic studies. We can be most grateful to Grabar for his yeoman services, which help to open the door to otherwise inaccessible information, and hope they can be continued. Apart from summary treatments of the year's progress in biochemistry, chemotherapy, etc., there are topical essays by: Sussman on the slime molds; DeVay on fungal mutualisms; McClung on anaerobes; Tomscik on immunocytology; Pontecorvo on parasexuality in fungi; and others of equal interest.

In my opinion, this volume and, judging from the forecast, the next one, have achieved a notable balance of emphasis that should be rewarded by a growing popularity of the series among microbiologists and indeed among biologists in general who require such glimpses into their neighbors' gardens.

J. LEDERBERG

INTRODUCTION TO BACTERIAL PHYSIOLOGY. *By C. E. Clifton. McGraw-Hill Book Company, New York, Toronto, and London.* $8.50. xi + 414 pp.; ill. 1957.

Twenty-five years ago, when Otto Rahn published his pioneering but still valuable book on the subject, bacterial physiology was a tidy little field. Its tidiness has been destroyed by the subsequent enormous growth of knowledge, and the first task of the teacher and writer today is to decide what limits, if any, he will set to the material offered to students as "bacterial physiology." Unless he is careful, he will find himself fighting hopelessly through the jungle of intermediary metabolism, or straying into enticing adjacent areas, such as cell structure and genetics. There is much to be said for reconstructing bacterial physiology as a limited field, centered on growth, and the nutritional and environmental factors which influence it. Bacterial growth is a fundamental and usually ill-taught subject, which can profitably form the basis for a course and a short textbook. To judge by current texts, however, the eclectic approach to bacterial physiology is still generally preferred.

The present book is typically eclectic. Nutrition and growth occupy only 2 chapters out of 18, and almost half the book is concerned with intermediary metabolism. There are chapters on physical chemistry, bacterial cytology, genetics, phage, chemotherapeutic agents, and the physiology of bacterial infectious diseases. The book is written at a relatively elementary level, and the author does not assume a prior knowledge of general biochemistry.

R. Y. STANIER

BERGEY'S MANUAL OF DETERMINATIVE BACTERIOLOGY. *Seventh Edition. By Robert S. Breed, E. G. D. Murray, Nathan R. Smith, and 94 contributors. The Williams & Wilkins Company, Baltimore.* $15.00. xviii + 1094 pp. 1957.

Since the publication of the first edition in 1923, Bergey's has been a useful, even indispensable, guide for the classification and identification of bacteria. There is little use to criticize the crude state of its methodology, whereby species and, indeed, genera and orders are divided upon bases lacking completely in genetic foundation; in large part, a lasting systematics of bacteria must await further development in the combined fields of microbial genetics, biochemistry, and immunology, and a wider appreciation of their significance in systems of classification.

With each edition, the manual has greatly improved as a practical guide and has increased its coverage of the microbial world. The convenient 2-column format of the 1948 edition is retained in the new edition. A large amount of supplementary data (inadequately described species, lesser synonyms, literature index, host-habitat index) has been relegated to a separate volume, *Index Bergeyana*. Much material of historical value and interest in the earlier editions has not been republished. Among innumerable revisions, most

notable is the addition of 5 new orders of the Schizomycetes (although one of these, the Mycoplasmatales, is of doubtful usefulness and, as work with bacterial protoplasts currently indicates, of doubtful validity). The formal classification of viruses has been omitted. While many of the changes appear worthwhile and will be lasting or at least will effectively aid the user of the manual, it is most disturbing to find other changes which serve no apparent purpose and no better fulfill a realistic classification than those used previously (e.g., the revisions in the Micrococcaceae).

PHILIP E. HARTMAN

MANUAL OF MICROBIOLOGICAL METHODS. *Soc. Amer. Bacteriologists.*

M. J. Pelczar, Jr., Chairman. McGraw-Hill Company, New York, Toronto, and London. $5.50. x + 315 pp. + 28 tables. 1957.

The bacteriologist will welcome this thorough compilation of important methods relating to the isolation, cultivation, storage, and characterization of bacteria and viruses. In replacing the loose-leaf *Manual of Methods for Pure Culture Study of Bacteria*, the book incorporates much of the old material and approach. Most of the material, however, has been brought up to date and broadened in its coverage and scope. New chapters on the maintenance and preservation of cultures, physiological and biochemical technics, and virological methods greatly improve the manual's over-all usefulness. One might wish for a little better guidance and further clarification of certain methods only cursorily covered; for example, the chapter on the detection of bacterial pathogenicity is especially of a very general nature, and yet refers the reader to general texts which are themselves no more informative.

PHILIP E. HARTMAN

PARASITOLOGY

FLEAS, FLUKES AND CUCKOOS. *A Study of Bird Parasites. Third Edition.*

By Miriam Rothschild and Theresa Clay. The Macmillan Company, New York. $5.00. xiv + 305 pp. + 40 pl.; text ill. 1957.

First published in England in 1952 (*Q.R.B.*, 28: 320. 1953), this book is now in its third edition, a status attesting to a surprising popularity for a work in a somewhat specialized field. Both writers are specialists in parasitiology who have published many excellent papers on the subject. The senior author is a member of the famous merchant banker family and a sister of Lord Rothschild, himself a distinguished zoologist.

In this volume the authors reveal to the general reader a generous glimpse into the world of animal parasites, with special reference to the parasites of the birds of Great Britain. As is true of the other volumes of the series with which I am familiar, the treatment is solid rather than superficial, and the style is both skillful and entertaining. Emphasis is placed upon parasitism as a widespread biological phenomenon developed through evolution. Although birds have been studied extensively, their parasites, especially the internal fauna, have received only sporadic notice, and the authors call attention to the unusual opportunities for research in this field.

Chapter headings include Parasitism, Commensalism, Symbiosis, The Effect of Parasites on the Host, The Effect of Parasitism on the Parasite, The Origins of Parasitism and the Evolution of Parasites, Fleas, Feather Lice, Protozoa, Worms, Flies, Mites, Microparasites, The Fauna of Birds' Nests, Skuas, and the European Cuckoo. In addition, there is a Bibliographical Index, an Index of Popular and Scientific Names, an excellent General Index, and an Index of Scientific Names of Birds mentioned in the text.

The authors consider symbiosis to be a close association of different species which derive mutual benefit from the relationship, whereas the writer prefers the term mutualism for this. Many biologists now think of symbiosis as "life together," the literal equivalent of the word, without commitment as to the advantage or disadvantage to the animals involved. The authors also broaden the term parasitism to include such social parasites as cuckoos. This is simply a matter of definition, but it points up the confusion which now exists over these and related ecological terms.

Referring to the handicaps of being a parasite, the authors state that "the chances of a grouse roundworm finding a grouse are far less than the reader's chances of becoming parents of quads, or a cabinet minister." Comparisons are drawn between the parasites and their free-living relatives in order to demonstrate the evolutionary changes in the former. Numerous examples are given to show the ubiquitous nature of parasitism. Problems of bird relationships are stated to be better understood in some cases if evidence from parasitism is considered. For example, the ostrich and rhea, now placed in separate orders, both are parasitized by species of a genus of feather lice found on no other birds, both have the same two species of mites, and both are hosts of subspecies of a tapeworm not found in other birds.

Protozoans, flukes, tapeworms, and nematodes of birds are given considerable attention, and the complicated life cycles of the worm parasites are discussed with special reference to their variety and possible origins and evolution. It is related that "when flatworms gave up their freedom, they certainly began an odyssey compared with which the voyages of Ulysses seem uneventful and commonplace."

Effects of direct parasitism and also the transmission of disease organisms by ecto-parasites are topics which receive brief treatment. Modification of flies and other groups, including the transition from a winged to a wingless form and modifications of reproduction receive attention. Bacteria, viruses, fungi, and the fauna of bird nests all come in for discussion, the chapter devoted to the latter being quite entertaining, for it seems that many bird domiciles are inhabited by a great variety of hangers-on like beetles, fleas, mites, ticks, moths, springtails, earwigs, booklice, spiders, and others. In fact, Nordberg in Finland, they write, recorded 529 different kinds of arthropods from the nests of 56 species of birds. It is therefore easy to agree with the authors that "even migration must seem a picnic in comparison with the tortures of nesting days."

In addition to the high-quality halftone plates, there are a number of good text figures. Photographs illustrate birds in their habitats, their parasites, and some of the special structures of the parasites.

Because this book deals with the principles of parasitism, supported by a wealth of interesting and pertinent data presented in an unusually readable manner, it is highly recommended to all parasitologists, and most biologists.

RALPH W. MACY

A MANUAL OF PARASITIC MITES OF MEDICAL OR ECONOMIC IMPORTANCE.

By E. W. Baker, T. M. Evans, D. J. Gould, W. B. Hull, and H. L. Keegan. National Pest Control Association, New York. $4.25. 170 pp.; ill. 1956.

During the past ten years more and more parasitologists, medical entomologists, physicians, veterinarians, pest control specialists, and others have been forced to deal with problems concerned with mites. Baker, who is the acarologist with the U. S. Department of Agriculture, is the man from whom most of these people attempt to gain information. In an effort to be of greater service, by making the answers to the most frequently asked questions more available, Baker asked Evans, Gould, Hull, and Keegan to cooperate with him in writing this *Manual*. The National Pest Control Association cooperated by publishing it.

The *Manual* contains figures and descriptions of all of the mites that commonly parasitize or bite man, his domestic animals, or his pets, including those mites that are vectors of disease. The life cycle, bionomics, and control of most species are also discussed. The *Manual* contains a key to the species that are discussed in it, but, as with all keys that cover only a few species of a large group of animals, it can be used only as a guide to what section of the book should be consulted to find out more about the specimens in question.

The book will be useful to specialists as a ready review of the information available about those species that are most frequently referred to them by physicians, veterinarians, pest control operators, householders, and others. For persons who have occasional problems with parasitic mites, such as medical entomologists and parasitologists, the *Manual* will answer most questions. The information is presented in concise form, and references to the more important or more recent publications on each species are given. Systematic and subject indexes are included.

G. W. WHARTON

DEVELOPMENT OF *HYMENOLEPIS NANA* AND *HYMENOLEPIS DIMINUA* (CESTODA: HYMENOLEPIDIDAE) IN THE INTERMEDIATE HOST *TRIBOLIUM CONFUSUM*. *Univ. Calif. Publ. Zool., Vol. 59, No. 9.*

By Marietta Voge and Donald Heyneman. University of California Press, Berkeley and Los Angeles. 75 cents (paper). Pp. 549–590 + 8 pl. 1957.

A SYNOPSIS OF HYMENOPTEROUS PARASITES OF MALACOSOMA IN CALIFORNIA: (LEPIDOPTERA, LASIOCAMPIDAE). *Univ. Calif. Publ. Ent., Vol. 14, No. 1.*

By Robert L. Langston. University of California Press, Berkeley and Los Angeles. $1.00 (paper). 49 pp. + 13 tables. 1957.

HEALTH AND DISEASE

NEOPLASMS OF THE DOMESTICATED MAMMALS. *Commonwealth Bureau of Animal Health, Review Series No. 4.*

By E. Cotchin. Commonwealth Agricultural Bureaux, Farnham Royal. 20s. xv + 100 pp. 1956.

The author presents a painstaking survey of his subject, and meticulously lists all the pertinent pathological data about mammalian neoplasms. The book contains an historical introduction, an adequate index, and is divided into 12 chapters, each on a different anatomical system under which reported neoplasms are discussed. There is very little discussion of epidemiology, pathogenesis, or possible therapy. However, the book contains one of the most complete bibliographies on the subject I have encountered. Chapter 14, although but 2 pages in length and devoted to obvious conclusions, concerns the "long recognized fact that there are important species differences in the frequency of neoplasms." This idea has been constantly pointed out in preceding chapters of the book and should be of great interest to any investigator attempting a species comparison of the incidence of neoplasms. This survey should also be of aid to the investigator who wishes to

conduct basic research on a particular anatomical neoplasm.

ROBERT G. CHAMBERS

DERMATOLOGIC FORMULARY. *From the New York Skin and Cancer Unit, Service of Dermatology. Revised Edition.*

Edited by Frances Pascher. Hoeber-Harper Books, New York. $4.00. xii + 172 pp. 1957.

This is an extremely practical and useful little book which has been developed over the years by the staff of the Skin and Cancer Unit of New York University Hospital and the Department of Dermatology and Syphilology of the New York Post-Graduate Medical School. It would be particularly helpful in any skin clinic to young physicians who are not thoroughly familiar with the prescriptions used daily in the practice of dermatology.

The only adverse criticism I have to make concerns itself with Directions for Care of Acne (p. 140). These Directions contain a restricted diet which is a relic of the 19th century, there being no controlled experimental evidence that supports the opinion that what one eats results in the outbreak of lesions of acne. Another Direction says, "Avoid constipation." But who has proved that constipation plays a part in acne? I think it is a mistake to perpetuate such unproved dicta. They engraft upon the minds of young people the erroneous idea that acne is the result of a fault in their own living habits, whereas nearly all evidence points toward a hereditary origin endocrine-actuated.

H. HANFORD HOPKINS

PSYCHOLOGY AND ANIMAL BEHAVIOR

BEHAVIOR MECHANISMS IN MONKEYS.

By Heinrich Klüver. The University of Chicago Press, Chicago. $6.50. xiv + 387 pp.; ill. 1957.

This book describes Klüver's pioneer studies of learning and perception in monkeys; the text is identical with that published in 1933. A new preface has been added.

J. M. WARREN

THEORIES OF PERSONALITY.

By Calvin S. Hall and Gardner Lindzey. John Wiley & Sons, New York. $6.50. xi + 572 pp.; ill. 1957.

This book is an expository survey of the major theories of personality. In preparing accounts of these theories, the authors made thorough searches of the literature and in many cases undertook correspondence with the theorists, with the result that the accounts, although condensed, are remarkably penetrating. Some of the theories actually seem to receive a more complete and lucid presentation here than is available elsewhere. Brief critical and evaluative discussions of the theories are also included, but no attempt is made at original theoretical development or synthesis of the theories.

CLINTON DE SOTO

AN INTRODUCTION TO CYBERNETICS.

By W. Ross Ashby. John Wiley & Sons, New York. $6.50. ix + 295 pp.; ill. 1956.

This book was written for workers in the biological sciences—physiologists, psychologists, and sociologists—who are interested in cybernetics and would like to apply its methods and techniques to their own specialty. An attempt has been made to keep the presentation as simple as possible, involving no mathematics beyond algebra.

Part I deals with the principles of mechanism and its representation by a transformation. It develops the concepts of "stability" and "feedback" and discusses the various forms of independence that can exist within a mechanism, and how mechanisms can be analyzed or synthesized. It goes on to study the principles that must be followed when the system is so large and complex (e.g., the brain or a society) that it can only be treated statistically. It also treats the case when the system is such that not all of it is accessible to direct observation—the so-called "Black Box" theory.

Part II uses the methods developed in Part I to study what is meant by "information," and how it is coded when it passes through a mechanism. It applies these methods to various biological problems.

Part III deals with mechanism, as used in biological systems for regulation and control, both in the born systems studied in physiology and in the learned systems studied in psychology. It provides an explanation of the outstanding powers of regulation possessed by the brain, and shows the principles by which a designer may build machines of like power.

An important feature of the book is the large number of problems, puzzles, and exercises (with answers in the appendix) drawn from a wide variety of fields.

This book should provide entertaining, though difficult, reading for most biological scientists. Many of the puzzles are clever and fun to work on, and there are some interesting ideas here. Another relevant question: will reading this book give the biological scientist some important new insights into his own subject matter? I do not think so.

A. CHAPANIS

THE PSYCHOLOGY OF CAREERS. *An Introduction to Vocational Development.*

By Donald E. Super. Harper & Brothers, New York. $5.75. x + 362 pp. 1957.

This book is oriented around the problems of why people work; the place of work in daily life and the life span; types of work; the course and cycle of the working life; and factors affecting vocational choice, success, and satisfaction. The basic material is drawn from psychology, sociology, and economics. Experimental and empirical data from these fields are carefully examined and implications drawn for both theory and practice. As a teacher at Columbia University, Donald E. Super has used much of this material in his courses, and the result is a well-organized book with many aids to facilitate reading. The liberal use of case studies from actual counseling situations adds concreteness. A very readable book, based upon sound scholarship, it should interest both the layman and the professional person.

A society which can pause to ask itself why people work is a sophisticated society. The answers in present-day America might range all the way from that which sees work as nothing more than the daily grind of making a living, largely incompatible with human freedom and dignity, to one which sees that man can realize himself only through work. Super's answer, based upon a large body of data and opinions, is that "satisfying human relations, activities that satisfy carried on in conditions which are agreeable, and an assured livelihood, are three major desires which men seek to satisfy in work." An occupation thus becomes more than a struggle for food, shelter, and clothing; it is a "way of life, a social role."

Indispensable to a psychology of careers is an occupational classification system to telescope the more than twenty-two thousand occupations into a few primary groups. Super calls attention to the inadequacies of all available systems, from the point of view of the vocational counselor, and suggests the possibility of a combination in which occupations can be described in three dimensions: the level of ability required, the field of activity or interest, and the enterprise in which it is carried on.

Matching intelligence, interest, and social status of a given individual to job requirements—what Super calls the "trait theory" of vocational guidance—should be supplemented, he says, by a theory of career patterns. Some of the most interesting chapters in the book are those concerned with the "self-concept." From the adolescent trying himself out in his first work experience, to the aging worker considering retirement, Super shows how the self-concept is related to career patterns, or vocational life stages. The development of a clear and realistic self-concept is a complicated process essential to vocational adjustment.

"Vocational guidance is," Super says, "the process of helping a person develop and accept an integrated and adequate picture of himself and of his role in the world of work, to test this concept against reality, and to convert it into a reality, with satisfaction to himself and benefit to society." Families, schools, and economic factors are all involved in the development of adequate career plans, in addition to the psychology of the person. The interaction of these factors with each other, with the individual as the battlefield where these factors struggle for resolution, is no easy matter for analysis. Super's patient examination of every bit of pertinent information and his synthesis of scattered research results in a consistent picture of vocational development.

One finishes Super's book with the thought that vocational guidance is coming of age. We do possess the knowledge and skills needed in optimizing the vocational adjustment of people; we do know how to use these skills; but we are nevertheless only at the beginning of a scientific system of vocational adjustment.

One addition may be made to this review which will be of particular interest to biologists. Super makes frequent reference (pp. 32, 41, 205, 235, 236, 238, 239, 245–247, 247–248, 278) to a study of Anne Roe's which appeared in 1951 as *Psych. Monogr.* 331 and was entitled *A Psychological Study of Eminent Biologists.* In this study she reported some things well known to biologists: that they work long hours in the office, laboratory, and home, on weekdays and weekends, and they would rather do biological work than anything else. That there is little difference in intellectual level of eminent and non-eminent biologists may be somewhat startling until the strong part played by motivation in achievement is remembered. Intellectual level is of course a factor in the selection of biology as a career. The following quotation (pp. 235–236) summarizes some of the personality characteristics which many of the biologists studied possessed.

> Biologists and physicists have been found to have no clearcut personality pattern, but something approaching one. They tend to see things as wholes, to generalize, and yet also to see details; they tend to be objective in their thinking; their interpersonal relationships tend to be smooth but not warm; they have a substantial degree of general anxiety; they tend to be unaggressive but stubborn, not dominant but not submissive. They tend to accept things as they are, but are intensely interested in knowing how and why they got that way. Like the artists she studied, Roe found these two types of scientists not high in masculinity, but better adjusted to life than the artists, partly, she believed, because they had more rational control and lived in a more stable and supportive social climate. The social life and work activities of the campus and research institute appear to stabilize marriage and life in general more than do those of the studio.

LUIGI PETRULLO

HUMAN BIOLOGY

THE HUMAN SPECIES. *A Pelican Book.* *By Anthony Barnett. Penguin Books, Harmondsworth (England), and Baltimore.* 5s. (paper). xiii + 334 pp.; ill. 1957.

I find it difficult to appraise this volume, which first appeared in book form in 1950. In the text Barnett refers at least twice to "Today, in 1954...." The references in the bibliography are mostly pre-1950. Since they are given separately for each chapter it is interesting to note that some chapters have post-1950, some post-1954, and some even 1957 references. Why some chapters have apparently been brought up to date and others not, is not clear. Moreover, some post-1950 text changes lack a bibliographic reference.

Despite an evident unevenness in treatment, I think this is a useful little treatise on "the biology of Man." The major headings indicate its scope: Part I: Heredity and Reproduction; Part II: Human Diversity; Part III: Life and Death. As might be expected, Part I, dealing as it does with basic genetics and embryology, presents information but little affected in the past decade. There is a good discussion of Lysenkoism. Part II reveals time-linked inadequacies. The Piltdown hoax is discussed, but Weiner's admirable report upon it is not referred to. Neither is the third Swanscombe bone mentioned. The S. African man-apes, split off in the Miocene, are shown as dead-end branches. Man is shown branching off in early Pliocene: there is no mention of *Oreopithecus*. Mayr's 1950 classification of *Homo transvaalensis*, *H. erectus*, and *H. sapiens* (including Neanderthal man) is not given. The cultural (archeological) classification is that of an older period; the more recent Clactonian, Chatelperronian, and Gravettian (following Movius and Braidwood) are not recognized. The major group category is four-fold: Negriform, Caucasiform, Mongoliform, Australiform. The discussion of race (sub-group) formation would have profited by reference to Coon, Garn, and Birdsell's *Races* (1950). Part III tends to follow doctrines of cultural evolution in discussing Man and Society. Chapters on food and soil, food and nutrition, physical and mental health, and population offer a well-rounded picture. The data presented here are fairly stable, though shifting population trends (longevity, numbers, and age-groupings) change decade by decade.

Any book trying to cover the human species biosocially sets for itself a tremendous task. Barnett, hampered by a certain unevenness in the selection of up-to-date material, has done a yeoman job. If I forego being a carping critic for the broader view of communication to the lay reader, then my final verdict must be, "well done."

W. M. KROGMAN

WHY CAN'T WE HAVE A BABY? *By James Henry Ferguson. Pyramid Books, New York.* 35 cents (paper). 127 pp. 1957.

Dr. James Henry Ferguson is well qualified to write a book on this subject, and his qualifications stand forth on each page of the succinct treatise. The author has a sympathetic, simple style. His ideas are progressive and not trammeled by convention. The book has a tendency toward oversimplification, and in some instances there is a slight distortion of fact in order to allay the infertile reader's fears. For example, Ferguson writes: "the statistical chances of a woman's becoming pregnant during the first year of marriage are not tremendous." Actually, several studies have shown that 90 in each 100 couples who achieve pregnancy do so within twelve months of the abandonment of contraception. Again we read, "a miscarriage is the death of the fertilized ovum, the embryo, in the first weeks of life and the expulsion from the uterus." This is not true, since perhaps 25% of abortions are alive when expelled.

In addition, I find myself in disagreement over several scientific points. Despite McLeod's studies on the positive correlation of coital frequency with conception, Ferguson extols the value of abstinence in improving the quality of a husband's semen. In outlining a healthful regimen for both partners he prescribes "some form of nonenervating out-of-door exercise." Now what proof is there that enervating exercise is anti-fertile? His suggestion that certain occupations, such as those of traffic policemen or skyscraper elevator operators, reduce fertility lacks substantiating data. In opposition to the author, I feel that the fate of vaginal spermatozoa in a post-coital test has little importance. The necessity for absolute immobility on the part of the wife after intercourse, to promote the chance for conception, is open to challenge. An important omission is the author's failure to note the role of tumors of the uterus (fibroids) and of congenital malformations in the problems of infertility and miscarriage.

Despite these criticisms, Ferguson has written an excellent primer for the unsophisticated reader on the subject of sterility. The book is up to date, unpadded, and simple. The next edition ought to include an index.

ALAN F. GUTTMACHER

EXPECTANT MOTHERHOOD. *Third Edition, Revised. By Nicholas J. Eastman. Little, Brown, & Company, Boston.* $1.75. vii + 198 pp.; ill. 1957.

This is an authoritative handbook for expectant mothers—and fathers. Simple and pleasantly readable, it conveys a great deal of information and can be highly recommended. First published in 1940 (2nd ed.,

Q.R.B., 23: 82. 1948), the present edition incorporates advances made in maternity care over the past decade.

EVELYN HOWARD

INDUCED ABORTION ON PSYCHIATRIC GROUNDS. *A Follow-Up Study of 479 Women. Acta psychiat., Kbh., Suppl. 99.*

By Martin Ekblad. Ejnar Munksgaard, Copenhagen. D.kr. 33.60 (paper). 238 pp.; ill. 1955.

Abortions have been legal in Sweden since 1946 if there are sufficient medical, social, humanitarian, or eugenical grounds. The extent to which this practice is carried on is indicated by the fact that in 1951 over 6000 abortions were performed. The present study deals with the case histories of 479 women who were granted abortions for psychiatric reasons, and it constitutes, in essence, a critical examination of the social effects of the abortion program on at least one segment of the population. Fifty-two of these women were also sterilized. Among the remaining married and single women there was a high recurrence (37%) of pregnancies within 22 months of the initial abortion, 84 of them unintentional. This sequel suggests, possibly, that sterilization should accompany abortion in many such cases since, in general, these women are relatively irresponsible and their children are not likely to receive the best of care. The problem, however, is not a simple one, and the author discusses all aspects with frankness and commendable objectivity.

FAMILY AND FERTILITY IN PUERTO RICO. *A Study of the Lower Income Group.*

By J. Mayone Stycos. Columbia University Press, New York. $6.00. xv + 332 pp. 1955.

"The raw material for this book comes from lengthy interviews with 72 husbands of the lower-income class and their wives: 24 from three rural areas, 24 from an urban area, and 24 from three small towns." Households were selected from a list including only houses valued at less than $250 by the Tax Assessment Bureau. The interviews took place from December, 1951, to March, 1952, the selections being from one region of the island. The treated topics include: Differential Status; Ideologies of the Sexes; Child-Rearing Practices; Courtship; Early Marriage and Consensual Union; Marital Relations; Attitudes toward Fertility: the Fertility Belief System; Attitudes toward Birth Control; Dynamics of Birth-Control Use; and Recommendations. A section on methodology, containing the forms used in interviews, appears in the book.

"In Puerto Rico . . . excessive population growth imperils the whole society." Birth-control methods are known to the poorer families and are practised to some extent. But traditional ideas and attitudes hamper wide use of them. That clinics be made physically more accessible to rural peoples is one of the author's recommendations.

WILSON D. WALLIS

SOCIAL THEORY AND SOCIAL STRUCTURE. *Revised and Enlarged Edition.*

By Robert K. Merton. The Free Press, Glencoe. $7.50. xviii + 645 pp. 1957.

It is difficult to write about this book except in superlatives, an unusual complaint among reviewers.

The author approaches and completes his task equipped with a rare combination of talents and insights: humanistic, historical, scientific, psychological, sprinkled through with large doses of down-to-earth common sense and uncommon acumen. It is theory pursued for the sake of enlightenment regarding factual matters.

The conviction is early expressed that theory should give us a better insight into facts, and accumulation of facts should lead to enrichment of theory. This point of view is consistently adhered to: "abstractions have a way of becoming unintelligible if they are not occasionally tied to concrete data" (p. 422). A "sociology of knowledge . . . requires not only an empirical investigation of the groups or strata which prevalently think in these terms, but also an interpretation of why these groups, and not others, manifest this type of thought" (p. 479). In this book sociology comes of age.

But a reviewer, to be worthy of his hire, must register some objections, even if he has to resort to trivia. The author has left his footnotes on the sands of time in such profusion that the conscientious reader is much too distracted from the main theme. Italics are too liberally sprinkled over the pages—a reader likes to discover for himself the proper emphases.

What we now need, following this considerable enlargement of the first edition of the book, is an abbreviation which would not be too formidable in number of words for the non-specialist who is interested in social life and methods of analysis—and what intelligent reader does not share that interest? There are pearls abundant, but only a plodding biologist would assume that he must have along with them a biography of each mollusk that produced them. Our reference to mollusks may be unjustified, for no one, I think, will deny that there are pearls here, and many of them. The 16-page chapter on The Self-Fulfilling Prophecy is worth many another entire book and deserves wide circulation.

WILSON D. WALLIS

THE THEORY OF SOCIAL STRUCTURE.

By S. F. Nadel; memoir by Meyer Fortes. The Free Press, Glencoe. $6.00. xvi + 159 pp. 1957.

If you enjoy abstractions, largely in the form of definitions, and logical deductions that can or cannot be made from them, without benefit of slices of reality, this is the book.

"We begin," says the author, "with the most general definition of 'structure' which underlies the use of the term in all other disciplines." (p. 7). "My definition and analysis of roles must include their 'basis,' the conditions entailing the 'further characteristics'." (p. 35). We learn that it requires several symbols on each side of the equation to demonstrate the fact that if A equals B, and B equals A, A and B "have equivalence." A "third level of abstraction is one at which relationships mean relative position and little else." (p. 108). A neat "formula represents a true sociological 'law'; for the circularity expressed in it is a fundamental aspect of prestige and similar states of social dignity." (p. 119).

One feels some sympathy for the student who endeavored strenuously and long to grasp the abstractness in *triad* and *dyad*, and triad so hard that he dyad. A more apt title of this book than the one given would be: A Theory of the Theories of the Structure of Social Structure. Meyer Fortes, who contributes a delightful Memoir, is "convinced that [the book] is destined to be one of the great theoretical treatises in the twentieth century social anthropology." I am more optimistic about the future of social anthropology.

WILSON D. WALLIS

DE OMNIBUS REBUS ET QUIBUSDAM ALIIS

INITIATION À LA MICROSCOPIE.
By Eugène Séguy. Éditions N. Boubée & Cie., Paris. 960 fr. (paper); 1,350 fr. (cloth). 253 pp.; ill. 1954.

A superficial introduction on the construction and operation of the microscope is followed by a long section describing preparative procedures for a wide variety of specific microscopic specimens. The amateur microscopist may find listed here a number of simple procedures which could suggest to him new materials amenable to microscopic examination and might guide him in his initial study of them. A third section, on accessory techniques and equipment, is so cursory as to be valueless.

PHILIP E. HARTMAN

BIBLIOGRAPHY OF MICROTECHNIQUE.
By Freda Gray and Peter Gray. Wm. C. Brown Company, Dubuque. $3.00. viii + 116 pp.; ill. 1956.

This reference volume may prove to be of value to those who require specialized information regarding microtechnique. It appears to be quite complete for material published in this field in the conventional European languages. Unfortunately, most of the information one would wish or need on microtechniques is already available from a relatively small number of almost universally distributed handbooks. One might doubt the wisdom of compiling such an extensive list of titles—most of which are obsolete—except for historical purposes. A critical omission here is the lack of listings in histochemistry and cytochemistry.

RONALD R. COWDEN

LECTURE NOTES ON THE USE OF THE MICROSCOPE. *Second Edition.*
By R. Barer. Charles C Thomas, Springfield, Ill. $1.50. vii + 76 pp.; ill. 1957.

Many medical and biological students do not receive adequate training in the use of an instrument they should know well. Barer has endeavored to correct this deficiency by supplying a beautifully clear and concise account of the fundamental principles of light microscopy. He stresses practical aspects of the proper use and care of the microscope, along with enough basic theory to make each point comprehensible. The material is presented in a manner which facilitates its use as an aid in class instruction. The second edition incorporates some minor corrections and additions, but happily retains the brevity, simplicity, and focus of the original edition.

PHILIP E. HARTMAN

TRAITÉ DE MICROSCOPIE. *Instruments et Techniques.*
By A. Policard, M. Bessis, and M. Locquin. Masson & Cie., Paris. 4,500 fr. (paper); 5,200 fr. (cloth). vi + 608 pp.; ill. 1957.

This ambitious volume has attempted to combine an extensive coverage of the instrumentation used in microscopy with a description of both general and specific preparation procedures used in biological research. The description of the theory and the practical considerations involved in the instrumental section are alike excellent. Although the chapters dealing with general staining methods are fairly complete, the sections dealing with cytochemical methods are not quite up to date. However, since it was the intention of the authors to present this volume as a general reference work, providing a skeleton of necessary information to the prospective investigator, it may be assumed that they have achieved this end. Its chief value to an English-speaking biologist will lie in its extensive coverage of microscopic instrumentation.

RONALD R. COWDEN

ANALYTICAL MICROSCOPY. *Its Aims and Methods in Relation to Foods, Water, Spices, and Drugs. Second Edition.*

By T. E. Wallis. Little, Brown & Company, Boston. $5.50. viii + 215 pp.; ill. 1957.

This book is an atlas as well as a manual of preparation for the microscopic examination of foods, water, spices, and drugs. As a result, it contains information that should be of interest to the agricultural scientist, sanitary engineer, forensic medical specialist, and pathologist. Throughout the book numerous pen-and-ink drawings are used to illustrate the various materials under consideration: seeds of weeds; desmids and algae; calcium oxalate crystals; pollen from honey; etc. A great deal of useful, if random, information is crammed into this little book, making it a worthwhile reference work.

RONALD R. COWDEN

EXPLORING WITH YOUR MICROSCOPE.

By Julian D. Corrington. McGraw-Hill Book Co., New York, Toronto, and London. $4.95. v + 229 pp.; ill. 1957.

This book is written for those who would like to take up microscopy as a hobby or an avocation. Its purpose is to introduce the reader to some of the main sciences; and to show both how the microscope is employed in each, and how a few of the slide preparations for each are made.

In the first part of the book, the author discusses the construction, principles, and care of the microscope, its operation and accessories. In chapters 5 through 13 the following fields are covered: microorganisms, textiles, geology and chemistry, insects, and detective work. Techniques of smears, embedding and sectioning, and staining are discussed. A bibliography of references is given at the end of each chapter. This book will be useful for an adult amateur microscopist working alone, and for an advanced high school or college student who would like to go beyond the material covered in a biology textbook.

MARY DEMEREC

THE QUARTERLY REVIEW OF BIOLOGY publishes critical reviews of recent researches in all of the special fields of biological science. The contribution should present a synthesis or digest of the researches and a critical evaluation of them. A mere synopsis of the literature without evaluation or synthesis is not desirable.

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Material ordinarily taking the form of footnotes is set in small print and placed in the text and consequently should be written in a style so as to fit readily into the text. Acknowledgments are printed in the text in small type at the end of the article just preceding the List of Literature. Recent issues of the Quarterly should be examined for style as regards (1) section or subsection headings in the text, (2) literature citations in the text, and (3) List of Literature.

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